TAXONOMIC STUDIES ON SUDAN ACACIAS

by

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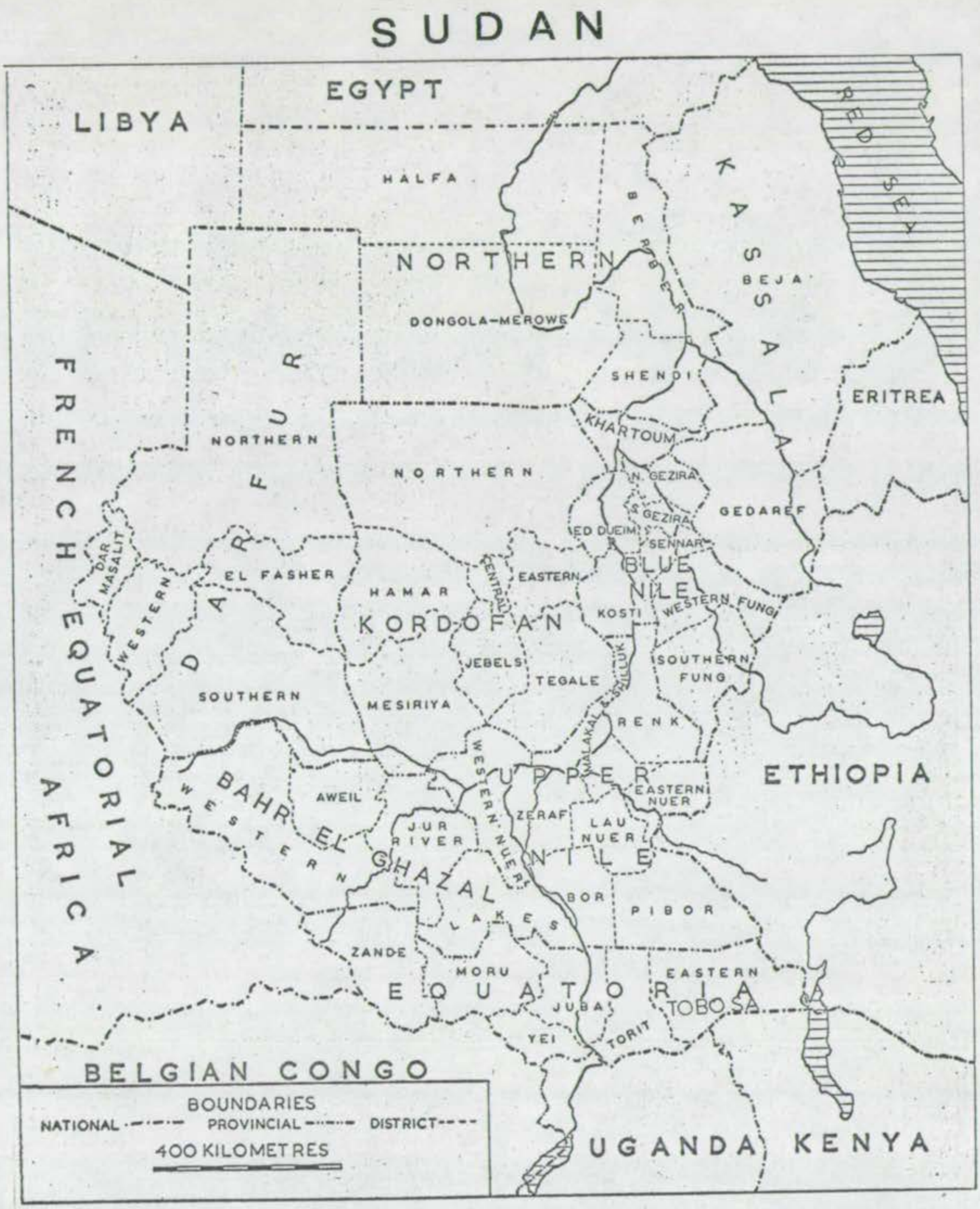
I. INTRODUCTION

1. GENERAL

Acacia species cover about two-thirds the area of the Sudan. They extend from tropical rainforests in the south, through deciduous savanna woodlands in Central Sudan, to the sub-deserts and deserts of Northern Sudan. These different habitats, grading from humid tropical conditions to dry desert conditions, provide good scope for a study of the genus.

The economic importance of the Acacias in the Sudan made this study a necessity. Their various domestic uses in the country contribute much to the national economy. In addition to the multiple local uses of the Acacias, their timber is used for furniture, buildings, railway sleepers, agricultural equipment, and as firewood and charcoal. Gum Arabic from A. senegal and other species produces an annual income of about £8m. Tannins for the leather industry are products from the pods, bark and leaves of A. nilotica and other species. A. albida is used as a shade tree for many agricultural crops, amongst which is tobacco. In an arid country like the northern and central Sudan, Acacia pods and leaves provide good fodder for domestic animals during the dry season. They are also utilised for many local medicinal purposes in the Sudan and other parts in Africa. In addition to these, soil reclamation measures use the Acacias to stabilize sand dunes. For these and other uses, the Acacias are worthy of a comprehensive study.

The Sudan species are spread all over Africa with other allied species. Other species of Asia and America are also allied to the African Groups. The Australian species, being largely phyllodic, are completely distinct from those in other continents. It is hoped that studying the Sudan species will offer good information on the genus and its members in large areas of the world excluding Australia.



MAP 1. GENERAL MAP OF THE SUDAN SHOWING NATIONAL, PROVINCIAL AND DISTRICT BOUNDARIES.

(FROM SUDAN SURVEYS TOPO NO S 813 - 55)

2. NOTES ON THE VEGETATION OF THE SUDAN

The following notes on the vegetation types of the Sudan are compiled from the personal notes I made during the many treks all over the country, either collecting specimens or doing other forestry activities. The earlier references on the Sudan vegetation are often consulted, amongst which the most prominent is the study made by Jackson and Harrison (1958). The vegetation belts are changing quickly with the change of micro climate and Man's activities, and consequently most of these belts mentioned in the previous works are not exact now.

The Sudan, a country of 1,000,000 square miles, extends from desert conditions in the north to high rainfall tropical forests in the south. The country lies between latitude 21° 55' N and 3° 53' N, and longitude 21° 54' E to 38° 30' E. It is bounded in the south by the Congo, Uganda and Kenya, on the east by Ethiopia and the Red Sea, on the north by Egypt and Libya, and on the west by Tchad and the Republic of Central Africa. Before describing the vegetation types, it is appropriate to give a brief account of the climate and soil types of the Sudan.

Rainfall

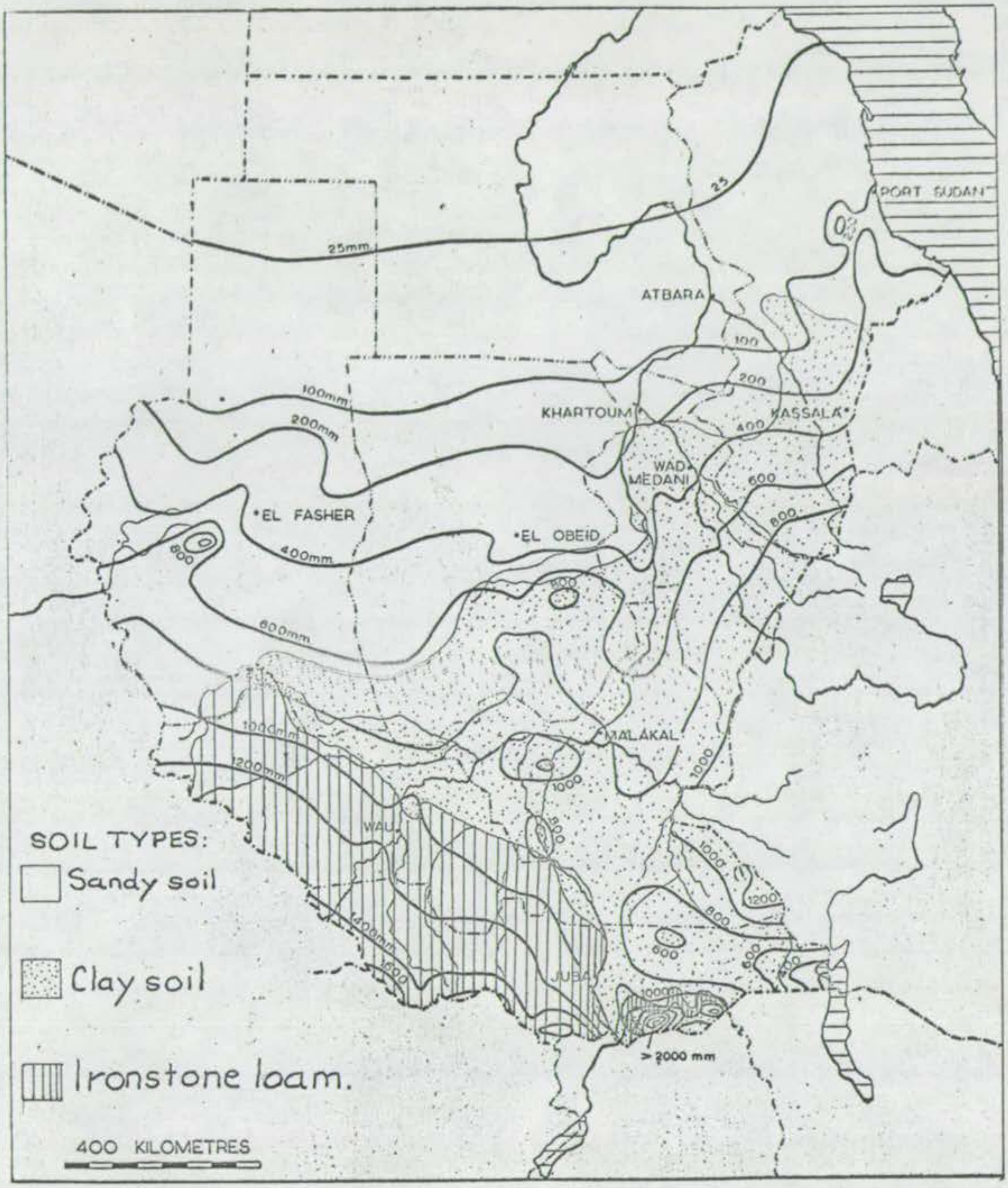
It varies from 0°mm in the Libyan and Nubian deserts in the north to 2,000 mm in the southern borders with the Congo and Uganda. The isohyets follow generally horizontal belts with few modifications due to altitude. In the highest rainfall areas in the southern borders, the rains fall almost all the year round. Proceeding northwards to Upper Nile, the rainy season is decreased to eight months with a dry period in December-February and a maximum of rain during the summer months of July and August. Going northwards to Central Sudan, the dry period increases from December to May or June, but with maximum rainfall again in August. Coming to the semi-desert area like Khartoum, the rains are confined to three months, July, August and September, giving a maximum rainfall of 100-200 mm. Proceeding to the desert north at Wadi Halfa, the rains are reduced to 0^{o} mm.

Winds and Temperatures

The north-easterly winds coming from the deserts blow in October to May, which is the dry season. These winds bring in the extreme cold and hot conditions of the deserts. The hot season extends from the end season of the north-easterly winds to June and July when the south-westerly winds blow, bringing the rains. The highest temperature during summer is $49.5^{o}C$ in the northern deserts and $46.1^{o}C$ in the tropical south. The lowest minimum temperatures vary from $7.8^{o}C$ at Wadi Halfa in the north to $10^{o}C$ at Wau in the south. There is an apparent change from day temperature to night temperature in North and Central Sudan, while in the south day and night temperatures are equable, together with temperatures throughout the year. This is due to the effect of rainfall and humidity, which is more abundant in the south than in Central and Northern Sudan.

Soils

These have a great influence on the vegetation types because of the water-holding capacity of different types of soils. The soil types are variable in the Sudan but can be generalised into three types : Sandy type, in Northern Sudan with low water-holding capacity and is alkaline; in Central Sudan we get the clay type, which is also alkaline, impermeable, but with a



MAP 2. MEAN ANNUAL RAINFALL IN MM AND SOIL TYPES.
(FROM SUDAN SURVEYS TOPO. NO. S 912 _ 54)

high water-holding capacity; in the Southern Sudan we get the acid ironstone types which are permeable but retain the water well. In addition to that we get the light silty soils along banks of rivers, streams, valleys and water depressions; they are fertile, rich soils, and have a high holding capacity of water.

Contour

Generally, the Sudan is a country of extended plains with few high mountains and hills. Usually these mountains and hills conform with the surrounding conditions except for a few high mountains, such as Jebel Marra in Darfur in Western Sudan, Imatong-Acholle range in Southern Sudan, and the Nuba and Red Sea Hills in Central Sudan. The northern parts consist of sand plains which are in permanent forms or loose sand dunes; a few hills (inselberges) occur scattered but with no influence on vegetation. The central clay and sandy plains are interrupted by J. Marra massif on the west, the Nuba mountains on the south-west, Angassana Hills on the south-east, and the Red Sea Hills on the north-east. In Southern Sudan occur gently undulating plains of the ironstone region, interrupted in the centre by the swamp or Sudd region of the White Nile. In the southern parts of Equatoria Province there are the high mountains of the Imatong-Acholle range, which rise to 2,400 m or more, and have a strong effect on the vegetation. An exceptional area in the south lies in the south-eastern border, called Tobosa, and consists of dark clay plains with low rainfall (about 600 mm) and resembles that of Central Sudan.

Vegetation types (see map 3 page 14).

The vegetation types of the Sudan are very much influenced by the effect of rainfall and soil texture (Smith 1949), in addition to the effect caused by Man's activities. There are five vegetation types which are well correlated with edaphic and climatic sequence from north to south, as follows :-

1. Desert (0-50 mm rainfall): This type lies north of 17°N but excludes the Red Sea Hills. It comprises both the Bayuda desert (Libyan desert) in the west and the Atbai desert (Nubian desert) in the east. Vegetation here is virtually absent except by watercourses as ephemeral herbs and grasses. A few stunted shrubs have spread from the semi-desert parts in the south and these include *A. tortilis* subsp. *tortilis*, *A. ehrenbergiana*, and the thorny *Fagonia arabica*. This desert area is crossed by the Nile where the vegetation types are modified into riparian vegetation with the presence of *Indigofera oblongifolia*, *Aerva javanica*, *Cassia acutifolia* and *Cassia aschrek*. Palms also exist in the Nile strip as well as in the desert oasis, like *Phoenix dactylifera* and *Hyphaene thebaica*. On the river banks occur *A. nilotica*, *A. albida* and *A. seyal*. Near the river grows a number of grasses, like *Desmostachya cyanosuroides*, *Panicum turgidum* and several *Aristida* species.

2. Semi-desert Acacia scrub and short grasslands (50-200 mm rainfall): This type of vegetation lies between latitudes 14°-17°N and includes the Red Sea Hills south of Toker and extends to north of Wad Medani and westwards to Dwem and El Gasher. It includes the Khartoum Province and the northern parts of the Gezina irrigated cotton area. Rainfall increases from north (50 mm) to south (up to 200 mm) with a drought period of about eight months. Annual and perennial grasses occur in scattered areas but these areas do not experience

grass fires. In this area shrubs and trees are more abundant and the Acacias constitute the chief floristic character, but the vegetation in general is scattered and vast areas may be without trees. Man's activities are very much intensified in this area and cause a lot of the patchiness of the vegetation.

This semi-desert zone has been divided into five sub-divisions (Jackson & Harrison 1958) :-

a) A. tortilis-Maerua crassifolia desert scrub in the east.

b) Semi-desert grassland on clay: Central part of the Botana and the Gezira regions where the dominant species are A. mellifera, A. nubica, Blepharis spp, Cymbopogon nervatus, Sorghum spp., Aristida spp., Tragus berteronianus and Setaria verticillata. Some herbs like Crotalaria spp. and Ipomoea spp. also occur.

c) Semi-desert grassland on sand: This constitutes the vast undulating sand-hills which compose the greater part of this region, with hollows in between the sand-hills. Here we get A. mellifera and A. tortilis subsp. raddiana, A. senegal, Commiphora spp., and Leptadenia pyrotechnica. The grasses are Aristida plumosa and Blepharis spp. In the east Cyperus conglomeratus occurs, and Enneapogon spp. in the west. Others are Cenchrus spp., Eragrostis tremula, Aristida spp., Schmidlia pappophoroides and Linum linifolium.

d) A. mellifera-Commiphora desert scrub: Found near rock outcrops. Other species are Boscia senegalensis, A. tortilis subsp. raddiana, Launea humilis and Indigofera spp. The annuals are Aristida spp., Schoenfeldia gracilis, Tetrapogon spathaceus, Panicum turgidum and Aristida plumosa.

e) A. asak-A. etbaica scrub: Found on the lower slopes of the Red Sea Hills. They form a community together, though A. etbaica disappears southwards.

Together with them and on the less lower slopes occur A. tortilis subsp. tortilis and A. tortilis subsp. spirocarpa, Delonix elata, Moringa aptera, Euphorbia cuneata, E. thi, Dracaena ombet, and Phoenix reclinata occur in Wadies.

3. Low woodland Savanna of Central Sudan (200-1000 mm): The area occupied by this type extends from latitude 10^{o}-14^{o}N, including Toposa area in South-East Equatoria. The soil is water-retaining and the drought period is 4-6 months, but the rainfall is sufficient to support many grasses and herbs and to maintain an open savanna woodland. The Combretaceous belt which stretches across Africa has its northern limit at the southern boundary of this region (Andrew 1948). The dominant trees are still the Acacias, but more broad-leaved trees are coming in. The open woodlands encourage the development of strong grass cover which causes frequent grass fires in the dry season, and accordingly all plants in this region are fire tolerant.

This type of vegetation is sub-divided into the following :-

a) Low rainfall woodland savanna, on clay: Consists mainly of short shrubs of the dry savanna dominated by Acacia species and covers the east central parts on clay soils, with A. mellifera as the dominant species. Other species occurring in this area are A. seyal, Balanites aegyptiaca on cracking clays, Commiphora Africana and Bascia senegalensis on hill soils. Cadaba glandulosa, Dichrostachys glomerata and Dalbergia melanoxylon also occur. Grasses associated with this type are Cymbopogon spp., Sorghum spp., Hyparrhenia pseudocymbrya, and Sehima ischaemoides. On the eroded soils of the Blue Nile and Atbara Rivers we get a clay soil supporting A. nubica, A. tortilis subsp. raddiana, Balanites aegyptiaca, and

Capparis decidua. The grasses include Aristida spp., Schoenfeldia gracilis, Setaria achromelaena, Sporobulus spp. and Cenchrus setigerus. As the rainfall increases from 200 mm to 570 mm, A. mellifera thornland changes gradually into A. seyal-Balanites savanna, and this in its turn passes gradually into the flooded region of Lake No with swamp vegetation of Cyperus papyrus and Voscia cuspidata. Here A. polyacantha subsp. campylacantha and A. sieberana grow along banks of the rivers and on areas liable to flooding and the two Acacia species replace A. nilotica, the dominant riverine species north of this flooded region. A. seyal var. fistula and A. drepanolobium occur on water depression areas on clay soils away from the river banks. Near the Blue Nile, on silty soils, the Acacia savanna is locally replaced by Combretum hartmenianum, Sterculia setigera, Sterospermum kunthiamum and Adansonia degitala. Along the Blue Nile and its tributaries, A. nilotica as well as on the White Nile until Lake No. On sloping grounds on the southern parts we get Combretum spp and Anogeissus woodlands mixed with A. seyal.

b) Low rainfall woodlands on sandy soils: This type constitute the vegetation of most of Central Kordofan and Darfur. We get A. senegal existing in pure stands and on the drier places it is mixed with A. tortilis subsp. raddiana, Leptadenia pyrotechnica, Maerua crassifolia. A. albida occurs here but on seasonal valleys and water collecting pockets.

c) Terminalia-Sclerocarya-Anogeissus-Prosopis Savanna woodland: When the rainfall rises from 600-1000 mm, broad-leaved trees appear and we get the Terminalia-Sclerocarya-Anogeissus-Prosopis savanna woodland which extends up to the southern limit of this zone.

d) Tobosa woodland Savanna: In the south-eastern corner of the Sudan occurs another grass area called the Tobosa. It resembles the semi-desert grasslands of Northern Kenya. It lies east of Toriet, latitude $4\frac{1}{2}^{o}$ to 6^{o}N. The rainfall is distributed erratically throughout the year, giving a vegetation of grasslands alternating with *A. mellifera* and *Balanites aegyptica* which resembles the thorn scrub of the Blue Nile. Other Acacias occurring are *A. horrida* subsp. *benadirensis*, *A. reficiens* subsp. *misera*, *A. paolii*, *A. elatior* subsp. *turkanae*, and the *A. tortilis* group. Along banks of streams occur *A. sieberana*, *Tamarindus indica* and *Kigelia aethiopica*. The area supports many grasses. Amongst them are *Chysopogon aucheri*, *Bothriochloa insculpta*, *Sehima nervosum*, *Themida triandra* and *Sporobolus helvokes*. This area is significant in being in Equatoria Province and having such dry conditions.

4. *Broad-leaved woodlands and forest region (1000-1500 mm)*: This includes the southern areas of Equatoria Province, west and east of the Nile and bordering Central African Republic, Congo and Uganda. The soil is the permeable red ironstone clay and the vegetation is the luxuriant broad-leaved closed forests with tall grasses, e.g. *Pennisetum purpureum*, *Urilytrum giganticum*. Trees are *Butyrospermum niloticum*, *Lophira alata*, *Combretum binadiranum*, *Terminalia mollis*, *Entada sudanica*, *Afzelia africana*, *Daniellia oliveri*, *Pterocarpus abyssinicus*, *Khaya senegalensis* and others. Along the Nile occur *A. sieberana*, *A. polyacantha* subsp. *campylacantha*. On the hilly ground we get *A. absyssinica*, *A. persciflora*, *A. macrothyrsa*, *A. macrostachya*. On the ironstone plains occur *A. kirkii*, *A. nilotica* subsp. *subalata*. The climbers *A. ataxocantha*, *A. brevispica*, *A. schweinfurthii* and *A. pentagona*, all occur

in moist closed forest areas and by streams on the hilly ground. Most of the Acacia species are concentrated on the eastern bank of the Nile.

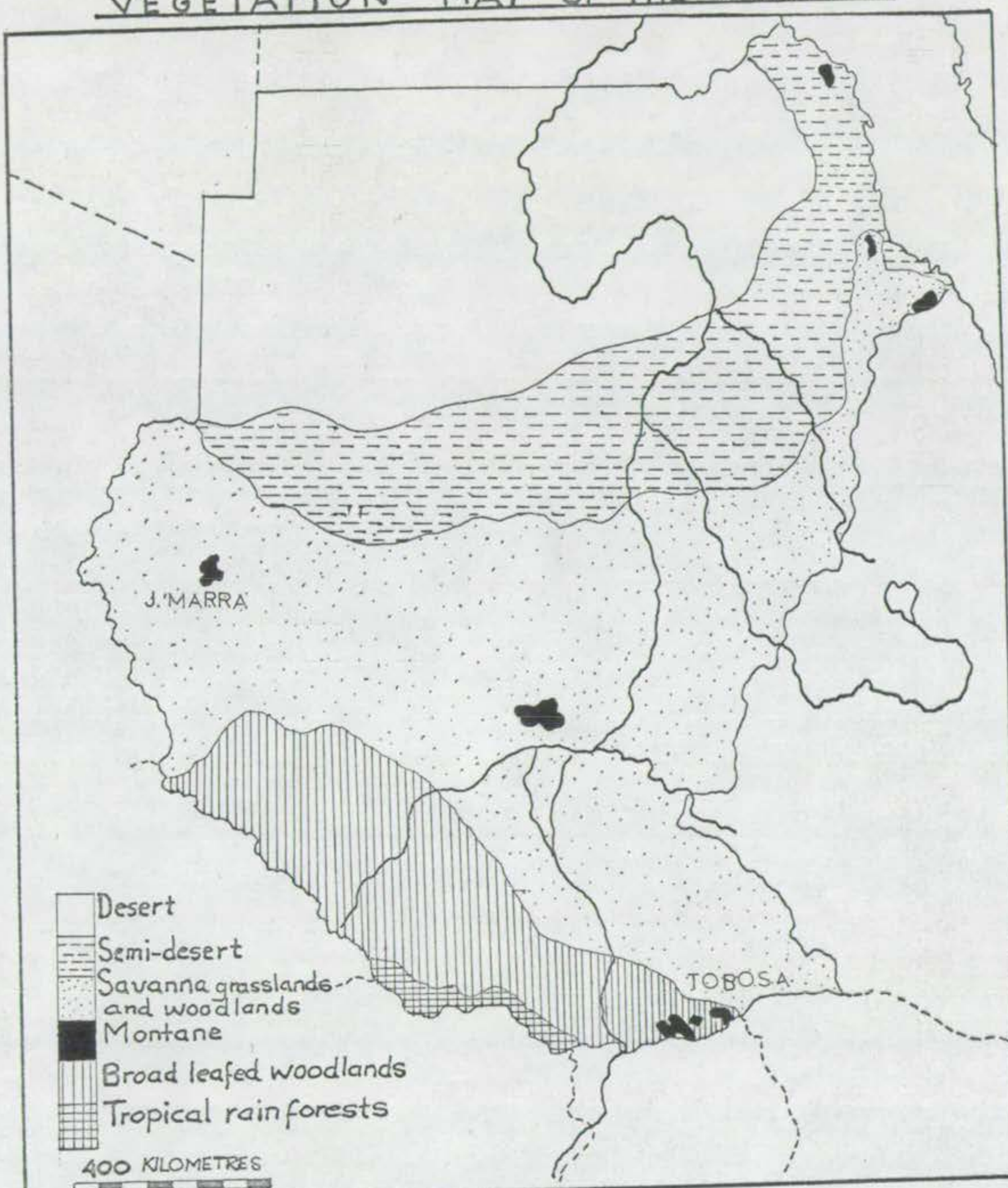
In the borders with the Congo we get a rainfall up to 2000 mm, especially on the Acholli Hills, and here we get the typical tropical rain forests of the Congo type.

5. Montane vegetation: The altitudinal effects on the vegetation are experienced in few areas. In the Equatoria Province, the Acholli Hills, namely Didinga, Latuke, Imatong and Dongotana Mountains, all lie east of the Nile, and in some of them the rainfall rises up to 2000 mm, giving luxurious vegetation cover, but in general resembles the Abyssinian montane vegetation with a few tropical African species. The Acacias occur in small areas on the slopes or at the foot of the mountains and some of these have been already mentioned in the previous type.

In Western Sudan, Jebel Marra (3250 m above sea level) has a modified vegetation as compared with its semi-desert surrounding. Broad-leaved trees occur together with other deciduous savanna species. The Acacias are mainly those of Central Sudan, though some of the high rainfall species also occur here like A. ataxacantha, A. sieberana and A. polyacantha subsp. campylacantha. A. albida is found at high altitude, at 2000 m, but in a shrubby form. The foot of the mountain is occupied by Acacias of the surrounding vegetation.

The Nuba mountains have a slight effect on the vegetation and few species of high rainfall areas occur. In the eastern borders with the Red Sea we get a range of Red Sea Hills covered with Abyssinian type of vegetation, e.g. Dracaena ombet, Aloe spp., Euphorbia spp., and Juniperus procera. The Acacias are limited to a few species, A. etbaica, A. asak and A. tortilis group.

VEGETATION MAP OF THE SUDAN.



MAP 3. MAJOR VEGETATION TYPES OF THE SUDAN

(FROM SUDAN SURVEYS TOPO. NO. S923 -55)

3. AIMS AND SCOPE OF PRESENT WORK

The Sudan has 31 native species of Acacia. They consist of trees, shrubs and climbers. They all have bipinnate leaves, and three infloresence types, spicate, capitate and sub-globose, are represented. There is thus a fair representation of the African range of the genus. This means that a revision of the Sudan species permits also a consideration of wider aspects of the genus as a whole. It is, therefore, the aim of the present account to revise the Sudan species and to use the information so gathered in a consideration of the general classification of the group.

In particular, the basic classification into spicate and capitate, already suspected of being artificial, has been critically studied, and as much other data (Palynology, Anatomy, Cytology, Seedling Developments) has been brought to bear on the problem as has been feasible in the time.

The individual species were studied to clarify their nomenclature, synonymy, and taxonomic status, and a special study of their ecology and distribution in the Sudan was undertaken. Characters, other than those of external morphology, were investigated in many fields for the first time as regards the Sudan species. A. albida, a controversial species, is fully investigated to clarify its position amongst the Acacias. A. laeta, a suspected hybrid, was also studied from different populations to ascertain its status.

These studies are based, not only on existing herbarium materials, but on personal field observations and collections of complete specimens, wood samples, bark samples, field photographs, etc., made by the writer during his work as Forester in different parts of the Sudan.

A natural classification is aimed at in this study, after a close look at as many characters as possible. The phylogeny of the Acacias is discussed here, though this aspect was hampered by the relatively small number of the species studied. However, from the available information on other groups in Africa, Asia, America and Australia, an attempt is made to interpret the results in an evolutionary manner.

4. PREVIOUS WORK ON THE SUDAN ACACIAS.

The taxonomic work on the Sudan Acacias has been of general floristic and morphological nature. Description and distribution of the species were precisely made by Schweinfurth (1867-8), Crowfoot (1928), Broun and Massey (1929) and Andrews (1952). The nomenclature in all mentioned studies was in confusion due to the many synonyms employed. Ecological and vegetational studies were carried out by Andrews (1948), Smith (1949), and Jackson & Harrison (1958). They all gave an account of the Sudan vegetation types, often in terms of presence or absence of Acacias. This provided a useful account of the distribution and ecology of the Acacias.

In 1966 Jackson wrote a field key to the Sudan Acacias based on morphological characters for the use of foresters in the field. He added records of 6 new species and made a good attempt to bring the nomenclature up to date. G. E. Wickens in 1968 produced additions and corrections to F. W. Andrew, Flowering Plants of the Sudan (1952). He provided the latest valid names of some of the Sudan Acacias, changing many of the names previously used in the Sudan floras and added a few new records from Western Sudan. In 1969 Wickens investigated the morphology and ecology of the controversial A. albida, and at the same time D. F. Cutter worked on the vegetative anatomy of the same species. Both studies emphasized the unique position of A. albida amongst the Acacias and its relation to the tribe Ingeae.

A few Acacia species were then described morphologically, according to their importance as forestry species, by W. C. Bosshard (1966) and K. C. Sahni (1968). Many other notes appeared on Acacias by the Forest Department of the Sudan, but none of these is of a taxonomic nature.

Thus, as is apparent from the previous work on the genus in the Sudan, there is no comprehensive taxonomic work on the Sudan Acacias. The genus still provides many complex botanical problems of classification and nomenclature in addition to the investigation of non-morphological characters. The fields of Cytology, Palynology, Anatomy and Seedlings development were never studied in the Sudan species before.

5. GENERAL WORK ON THE GENUS ACACIA

Linnaeus (1753) described five species of Acacias under the genus Mimosa and separated them by the characters of the stipules. It was P. Miller in 1754 who gave the name Acacia to the genus. Willdenow (1806) in his Species Plantarum was the first to sub-divide the large Linnaean genus Mimosa, based on fruit characters, into Mimosa and Acacia and described 102 species of Acacia.

In 1813 Delile described three Acacia species from Egypt, namely A. albida, A. seyal and A. nilotica.

De Candolle (1825) cited ten species from West Africa and classified them according to inflorescence characters. Then West and North African species were studied by Hayne (1825), Schumacher (1827), Savi (1830) and Guillemin, Pervottet and Richard (1832).

It was not until Bentham's account (1842) that detailed work on Acacia and its classification was started on a world basis. In his third revision of the Mimosaceae (1875), he divided the genera in the family into three tribes based on the floral characters. The tribe Acacieae was distinguished from the other two tribes by having "stamens all free or the central ones united at the base". He then proceeded to divide the Acacieae into six series based on vegetative habits, and geographical regions, with the reproductive organs accorded less importance. Bentham stated in his third revision of the genus Acacia "I have not either been able in this my third careful revision of the species to divide it into sections founded upon any character derived from the flower or fruit". His classification is important because most of the recent classifications are modifications of Bentham's work. Bentham's six series are as follows:-

Series I Phyllodineae:

Leaves reduced to phydodia or minute scales without leaflets.

Endemic to Australia. Sub-divided into 8 species.

Series II Botryocephalae:

Stipules small or absent; leaves bipinnate. Inflorescence globose.

Endemic to West Australia.

Series III Pulchellae:

Stipules none or small, setaceous, non-spinescent; leaves bipinnate. Inflorescence cylindrical spikes or globose.

Western Australia.

Series IV Gummiferae:

Spinescent stipules; leaves bipinnate.

subseries 1:- Summibracteatae: Involucel at upper part of peduncle.

subseries 2:- Medibracteatae: Involucel at middle part of peduncle.

subseries 3:- Basibracteatae: Involucel at basal part of peduncle.

In Africa, Asia and America.

Series V Vulgares:

Non-spinescent stipules. Prickles scattered to rare or even absent; leaves bipinnate. Inflorescence spikes or globose.

subseries 1:- Gerontogeae spiciflorae

A Triacanthae

B Diacanthae

C Ataxacanthae

subseries 2:- Americanae spiciflorae

subseries 3:- Americanae capitulatae

subseries 4:- Gerontogeae capitulatae

Endemic to Africa, America and Asia; absent in Australia.

Series VI <u>Filicineae</u>:

Shrubs, unarmed, pubescent or glabrous; leaves bipinnate; petioles eglandular. Inflorescence in globose heads. Endemic to Mexico.

Bentham studied 434 species of Acacia, the Sudan species being included in his Gummiferae and Vulgares series.

Schweinfurth (1867-8) on his work on the Acacias, dealt mainly with the Sudan and Abyssinian species. He followed Bentham's series, the Gummiferae and the Vulgares, but he used the inflorescence to separate the Acacia groups.

Taubert (1894) followed Bentham's classification and so did Burkart (1952) later on.

The later workers on African Acacias, Oliver (1871), Hutchinson and Dalziel (1927), and Baker (1930), all considered the inflorescence to be most important in grouping the species, and they based their classification according to spicate versus capitate, with the vegetative characters given lesser importance.

Harvey (1894), Glover (1915), and Roberty (1948), considered the characters of the stipules as more important than the others and produced their own classifications accordingly.

In 1932, I. V. Newman, while working on the Australian Acacias, rejected completely the classification concepts put forward by Bentham and other workers. He created his own original groups which were based on the inflorescence, flower groups, and (coming last) vegetative characters; he claimed that his classification was phylogenetic. His classification is as follows:-

I	Racemoseae (Inflorescence in racemes).		
II	Constateae (	"	clustered).
III	Singulares (	"	single).

Each of these groups is sub-divided according to the flower shape:

i	Spicateae (Flowers in cylindrical spikes).			
ii	Oblongae (	"	"	oblong spikes).
iii	Globulae (	"	"	globular heads).

A further sub-division of these depends on the foliar type:

1. Phyllae (True leaves. Bipinnate in adult of present day).
2. Phyllodineae (Petioles without lamina in adult).
3. Phyllocladineae (Entire absence of leaves).

This classification can hardly be considered as natural, being based mainly on the inflorescence types.

Brenan in his Fl. Trop. East Africa (1959) and Fl. Zambeziaca (1970) produced detailed morphological studies on East and Central African Acacias and their infraspecific variants. He made artificial keys based on the inflorescence and vegetative characters, and another key of the pod characters together with vegetative attributes. He also produced artificial groups to facilitate their separation in East and Central Africa. Many of the Sudan species are included in his study. He stressed the fact that more comprehensive investigations are needed to produce natural groupings. However, his work is important because it gives a good description of the individual species and the delimitation of infraspecific groups. He also made a study with A. W. Exell (1957) on the A. pennata group, or the climbing capitate Acacias, but did not include A. ataxacantha within them.

Another worker on African Acacias is J. H. Ross (1966), who studied South African species; he adopted the inflorescence classification for its ease of identification, though he mentioned that the inflorescence classification could be artificial. His work was mainly morphological, based on population studies and the extent of the species variations.

The work on the American Acacias was made by Britton and Rose (1928), who returned to the character of the fruits (which was used by Willdenow in 1806). They divided the Acacias into 12 new genera but this classification was not accepted by later workers, and has faced many criticisms.

Though not much work was done on microcharacters, a few isolated cytological studies on some Acacias were made by Ghimpu (1929, 1930), Senn (1938), Atchison (1948), Khan (1951), and Sharma and Battacharya (1958). Their work is often difficult to interpret, due to erroneous synonymy. Yet certain facts emerged about the basic chromosome number as 13; the diploid 26 is represented by the Australian and Vulgares series and the polyploid 52, 104, 208, apparently confined to the Gummiferae series.

Palynological investigations on a few Acacias were carried out by Mohl (1834), Rosanoff (1866), Wodehouse (1934), Selling (1948), Cookson (1953), and Coetzee (1955), but again too many synonyms were involved. However, they all agreed on the compound polyad as characteristic of the Acacia pollen.

It is only recently that Guinet (1969) has made an extensive work on the palynology of the Mimosaceae. He recognised three groups of the Acacias based on their pollen types, namely :-

I Vulgares and Filicinae

II Phyllodineae, Pulchellae and Botryocephalae

III Gummiferae

Guinet held the view that the Vulgares and the Filicinae are the ancient groups and are more related to the Australian groups than the Gummiferae. The latter is a well defined group which has evolved into diploids and polyploids and seems to be the most differentiated group. His conclusions fit well with Benthams classification, but are strongly opposed to Newmans, and disagree with Atchison's view of the Gummiferae, which he believed to be the most primitive group.

In the field of anatomical investigations not much work was carried out. Timber anatomy is the least investigated, except for a few papers which separate A. albida from the others; this was done by Chevalier (1928) when he decided to include A. albida (Faidherbia albida) in the tribe Ingeae. A more detailed anatomical study of A. albida was carried out recently by Cutler (1969). Some nodal anatomy investigations were undertaken by Watari (1932-36) on Leguminosae stipules which have also been studied by other authors, e.g. Sinnott (1914), Dormer (1944), Metcalfe & Chalk (1952), but they all dealt with the anatomy of the whole order Leguminosae.

The study of the seedling development of the Acacias started with Cambage (1915-16). Working on the Australian species he showed that the first leaves are pinnate, followed by bipinnate leaves and finally phyllodes. Vassal

(1963-7) continued the work with species from Australia, Africa, Asia and America, and grouped their developmental patterns into three types:-

Pattern 1: 1st leaf pinnate, 2nd leaf pinnate, 3rd leaf bipinnate.

Pattern 2: 1st leaf pinnate, 2nd leaf and 3rd leaf bipinnate.

Pattern 3: 1st, 2nd and 3rd leaf bipinnate.

In the Gummiferae group he found patterns 1 and 2 and in the Vulgares patterns 1, 2, and 3.

Recently Robbertse and Van Schijff (1971) worked on seedling development and suggested certain phylogenetic trends, and raised the capitate climbers to a "sub-order" Farinosae.

6. SYNOPSIS OF GROUPS IN ACACIA

The following table shows the Sudan species under investigation, arranged in the traditional classification into spicate and capitate groups.

TABLE NO. 1

Spicate inflorescence	Capitate inflorescence
Acacia mellifera Benth.	A. sieberana DC.
A. laeta Benth.	A. abyssinica Benth.
A. hecatophylla A. Rich	A. reficiens Wawra
A. polyacantha Willd.	A. elatior Brenan
A. macrostachya Reichenb.	A. etbaica Schweinf.
A. persiciflora Pax.	A. nubica Benth.
A. asak Willd.	A. tortilis Hayne
A. senegal Willd.	A. drepanolobium Sjostedt
A. ataxacantha DC.	A. gerrardii Benth.
A. horrida Willd.	A. paolii Chiov.
A. albida Del.	A. macrothyrsa Harms
	A. seyal Del.
	A. hockii De Wild
	A. ehrenbergiana Hayne
	A. nilotica Del.
	A. kirkii Oliv.
	A. brevispica Harms
	A. schweinfurthii Brenan & Exell
	A. pentagona Hook.
A. dolichocephala	

This grouping based on the infloresecence types has been suspected by many workers of being artificial, and indeed it has been shown to be so. A. horrida, which is placed with the spicate group, has no affinity at all with the members of this group and is allied with the capitate group. A. albida, though different from all the Acacias, is allied with the capitate group but very different from the members of the spicate group. On the other hand, the three climbers, A. brevispica, A. schweinfurthii and A. pentagona, placed in the capitate group, have no affinity with members of this group but are related to the spicate group, especially with A. ataxacantha. A. dolichocephala, having a sub-globose infloresence, does not fit in this classification, being intermediate in infloresence characters; it is in fact related to the capitate group and is very distinct from the spicate group.

However, many workers have used the infloresecence groupings, even to the present day. Amongst these are Oliver (1871), Schweinfurth (1867), Baker (1926-30), Hutchinson and Dalziel (1927-28 and 1958), Burtt Davy (1932), Aubreville (1933), Newman (1933), Andrews (1952), Exell and Mendonca (1956), Brenan (1959), Dale and Greenway (1961), White (1961) and Ross (1971).

Other authors working on the Acacias classified them according to vegetative characters, such as Bentham (1842), Harvey and Sonder (1894), Thonner (1915), Chevalier (1928), Roberty (1948), Aubreville (1950), Guilbert and Boutique (1952), and Jackson (1966).

According to the results of my study, the vegetative characters, especially those derived from the stipules, give a more natural classification supported by much evidence from palynology, anatomy and seedling development. Thus four subgeneric groups are suggested here. Three of them have distinct stipule characters in addition to other correlated attributes, and the fourth group consists of A. albida which holds an isolated position. The inflorescence type, striking as it is, does not play a significant part in this classification.

For ease of reference in this thesis, this new classification is presented here with reference to the following lists; the capitate Sudan species (C) or spicate (S) nature of the inflorescence is indicated for each species. This classification will be substantiated as the thesis proceeds.

Group I:

Stipules spinescent. Pod venation longitudinal, oblique or not apparent, usually constricted and not compressed. Spines at nodes usually white, straight and having a vascular system. Inflorescence globose heads, cylindrical spikes and sub-globose heads. Flowers hermaphrodite, sometimes male flowers also occurring, white-cream, yellow or orange. Stamens glandular, free. Ovary shortly stipitate. Seeds oblong with a U or O-shaped marginal areole. Pollen grains in polyads (16-celled) with 3 fissures and 3 pores. 2n = 26, 52, 104. Trees and shrubs. Distribution all over the Sudan.

This group includes the following species:

1. A. sieberana (C)
2. A. abyssinica (C)
3. A. elatior (C)
4. A. reficiens (C)
5. A. etbaica (C)

6. *A. nubica* (C)
7. *A. tortilis* (C)
8. *A. drepanolobium* (C)
9. *A. gerrardii* (C)
10. *A. paolii* (C)
11. *A. macrothyrsa* (C)
12. *A. seyal* (C)
13. *A. hockii* (C)
14. *A. ehrenbergiana* (C)
15. *A. nilotica* (C)
16. *A. kirkii* (C)
17. *A. dolichocephala* (sub-globose)
18. *A. horrida* (S)

Group II:

Stipules non-spinescent, membranaceous-filiform. Pod venation horizontal; not constricted, compressed. Prickles at nodes in pairs, usually dark brown, falcate and having no vascular system. Inflorescence cylindrical spikes. Flowers hermaphrodite, pink or white-cream. Stamens glandular, connate at base. Ovary shortly stipitate but with a slightly longer stipe than Group I. Seeds orbicular, areole central and crescent-shaped. Pollen grains in polyads (16-celled) with 4 pores and no fissures. 2n = 26. Trees and shrubs. Distribution South and Central Sudan, absent in Northern Sudan.

This group includes the following species:

1. *A. Mellifera* (S)
2. *A. laeta* (S)

3. A. hecatophylla (S)
4. A. polyacantha (S)
5. A. macrostachya (S)
6. A. asak (S)
7. A. senegal (S)

Group III:

Stipules non-spinescent, foliate. Pod venation horizontal; not constricted, compressed. Prickles scattered on internodes and rachis, dark brown, falcate, and having no vascular system. Inflorescence cylindrical spikes and globose heads. Flowers hermaphrodite, white-cream. Stamens glandular, connate at base. Ovary with a long hairy stipe, longer than ovary. Seeds orbicular to oblong; areole crescent-shaped or U-shaped, central or marginal. Pollen grains in polyads (16-celled), smaller in size than in Group II, with 4 pores and no fissures. $2n = 26$. All climbers. Distribution in Southern Sudan and round Jebel Marra in Western Darfur. Absent from Central and Northern Sudan.

This group includes the following species:

1. A. brevispica (C)
2. A. schweinfurthii (C)
3. A. pentagona (C)
4. A. ataxacantha (S)

Group IV:

Stipules spinescent. Pod venation longitudinal or not apparent, not constricted, not compressed. Spines short, white with brown tips, and having a vascular system. Inflorescence cylindrical spikes. Flowers hermaphrodite, white-cream. Stamens eglandular, connate. Ovary stipitate. Seeds obovate, areole U-shaped, marginal. Pollen grains in polyads (28-32-celled) with 4 pores and no fissures; largest in the genus. 2n = 26. Tree. Distribution all over the Sudan.

This group includes only one species:

1. A. albida (S)

This synopsis into four groups can probably be extended to cover all Acacia species native to Africa, and most American and Asian species.

II STRUCTURE OF THE ACACIAS

A. MORPHOLOGICAL CHARACTERS USED IN THE BASIC CLASSIFICATIONS

1. Habit and form

Sudan Acacia species are deciduous plants; they mostly shed their leaves in the dry season (November-May) and retain them during the rainy season (June-October). The exception is A. albida which sheds its leaves during the rainy season and retains them in the dry season.

The habit of the Acacias varies from shrubs or small trees with flat crowns (umbrella-shaped) like A. tortilis subsp. tortilis and A. nubica; round crowns like A. mellifera and A. laeta to irregular crowns of A. ehrenbergiana; trees with round to irregular crowns; climbers on other big trees like A. brevispica and A. ataxacantha. The majority of the Acacias are shrubby, few are big trees and fewer climbers. The ecological habitats have great effect on the form of the species as a large tree like A. albida may have a shrubby form on high altitudes, as in Jebel Marra. A. seyal has many forms, getting smaller and more shrubby as it moves towards the dry arid regions. The climbers can also exist as independent shrubs if they grow in bare ground without supporting trees.

A main stem exists on the tree species, while on shrubby forms the stems can be 2 to many branching from the base. (See Plate 1 page 33).

2. Bark

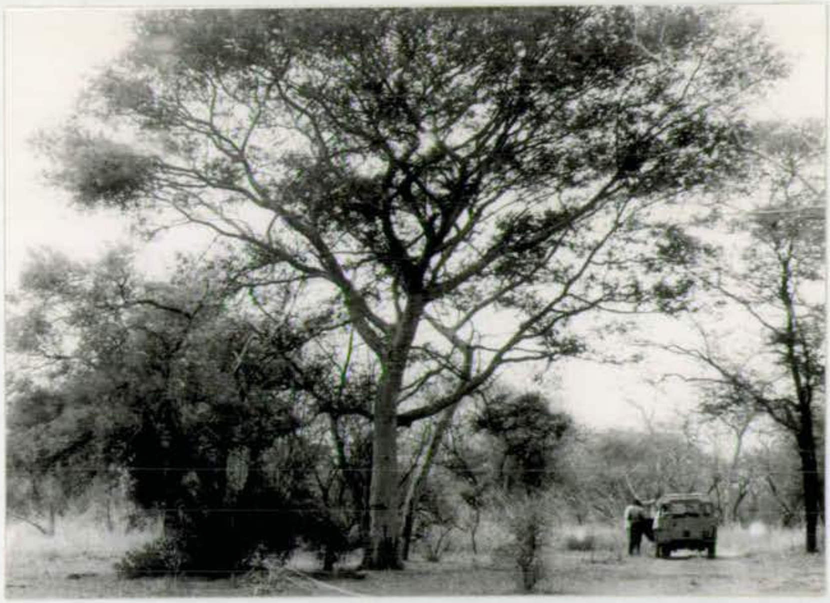
Most of the Acacias have fissured, dark or pale grey bark, e.g. A. nilotica and A. gerrardii. Acacias in the dry zones have a smooth bark which may help in conserving the water inside the tree. A few Acacias

Plate 1. Habit and form of the Acacias.

a. <u>A. sieberana</u> (x $\frac{1}{220}$). Tree, main stem, round crown.

b. <u>A. ataxacantha</u> (x $\frac{1}{50}$). Climber, main stem, spreading crown.

c. <u>A. ehrenbergiana</u> (x $\frac{1}{40}$). Shrub, many stems, irregular crown.



Pl.1

Plate 2. Bark characters.

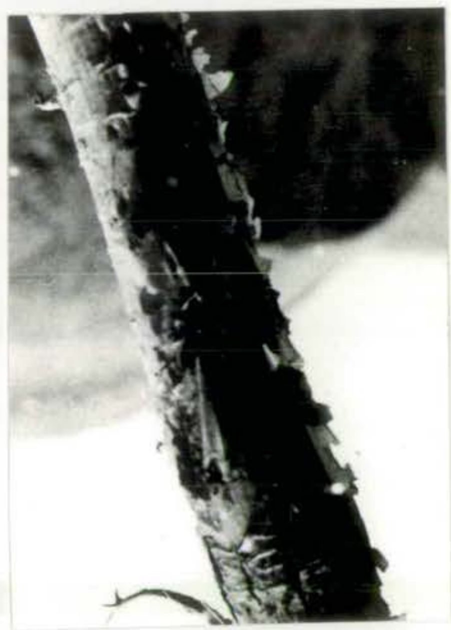
a. A. gerrardii ($\times \frac{1}{6}$). Rough and fissured.

b. A. seyal var. seyal ($\times \frac{1}{6}$). Smooth.

c. A. asak ($\times \frac{1}{6}$). Flaking.

a

b



c

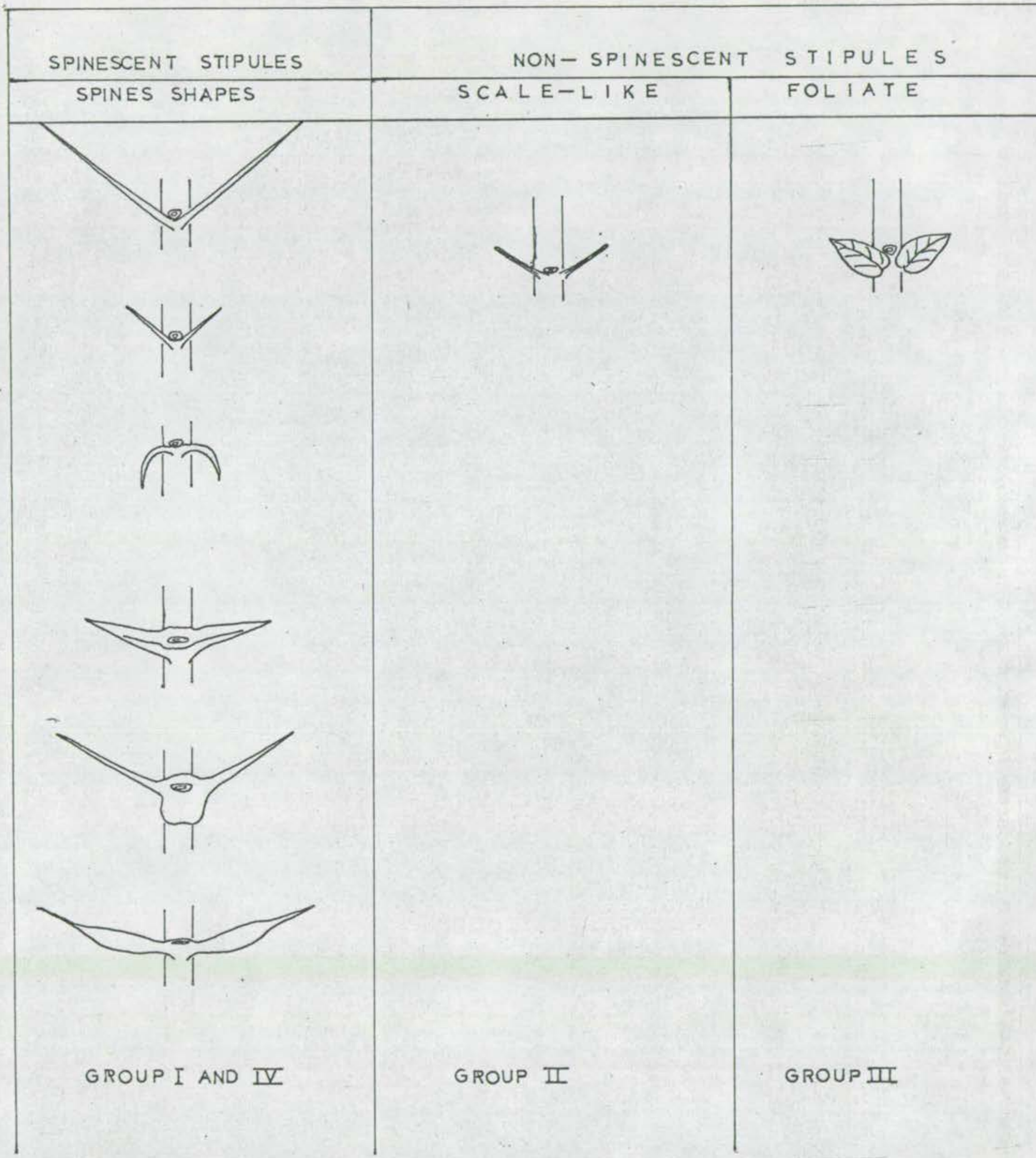
Pl. 2

have diagnostic bark characters like A. seyal, which has a powdery bark of red-brick colour, or powdery yellow-green colour, as in A. seyal var. fistula. A mixture of both red-brick and green colour can exist in the bark of A. seyal var. seyal. A. ehrenbergiana and A. asak have a yellow flaky bark on their branches. The young branches of A. albida have a milk-white bark but the old main stem has slight fissured light grey bark. The climbers usually have a light grey flaky bark. A. kirkii, occurring on banks of streams, has a green bark. A yellow smooth bark is characteristic of A. polyacantha subsp. campylacantha, but as the tree ages, or under moist conditions, the bark turns rough and grey. A. sieberana var. sieberana can have a light greyish-yellow smooth bark and again may become fissured in moist habitats, as with its two varieties vermoesenii and villosa. Thus the bark can be characteristic of certain species under certain conditions but cannot be relied upon to separate species or groups (Plate 2 page 34).

3. Stipules

The character of the stipules is the most important feature in separating the groups in the Acacias. The Sudan and African species are all stipulate. One group of the Acacias, the climbers (Group III), retains the stipules in a foliaceous form. Group II has its stipules which are scale-like or membranaceous-filiform; they are usually soft, colourless or pale green. In both these groups the stipules are non-spinescent and caducous, falling off when the leaves are mature. Group I has its stipules modified into persistent spines; they are hard, usually white to yellow or brown tipped; in most cases they are straight but in a few species they are hooked or curved spines. They are persistent.

FIG.1 ACACIA STIPULES:



Anatomically they all have the same basic structure. A. albida, which is included in Group IV, has spinescent stipules which are persistent and similar to those in Group I. The foliate type of stipules of the climbers (Group III) is found in both capitate and spicate species in the group. The scale-like membranaceous-filiform type of Group II is found is spicate species which are the only members of Group II. The spinescent type is found in spicate, capitate and subglobose species of Group I.

4. Spines and prickles

Sudan Acacias are all armed with either spines or prickles.

The climbers (Group III), which have retained their stipules unmodified in foliate forms, have developed falcate prickles which are scattered on the internodes, rachis and sometimes on rachilla. Group II has developed prickles on the nodes but occasional prickles may appear on the internodes or rachis; the normal occurrence of prickles is on the nodes and in pairs or threes. Group I, as mentioned before, has stipules modified into spines which are always in pairs and on the nodes only. Thus two types of armature are formed: the prickles, which are non-spinescent, falcate, borne on nodes, internodes, rachis and rachilla, in twos, threes or scattered; they are dark brown, have no vascular system and are of exogenous origin. On the other hand, the spines are spinescent stipules, straight, rarely hooked, on nodes, white to brown, in twos only, have a vascular system and are of endogenous origin. (See page 38 fig. 2 & page 39 fig. 3).

Members of Group I all have spines, irrespective of the type of the inflorescence. A. albida of Group IV has spines also. Group II, which has prickles, are all spicate species, while Group III, which has prickles, are spicate and capitate. Thus the development of prickles and spines has

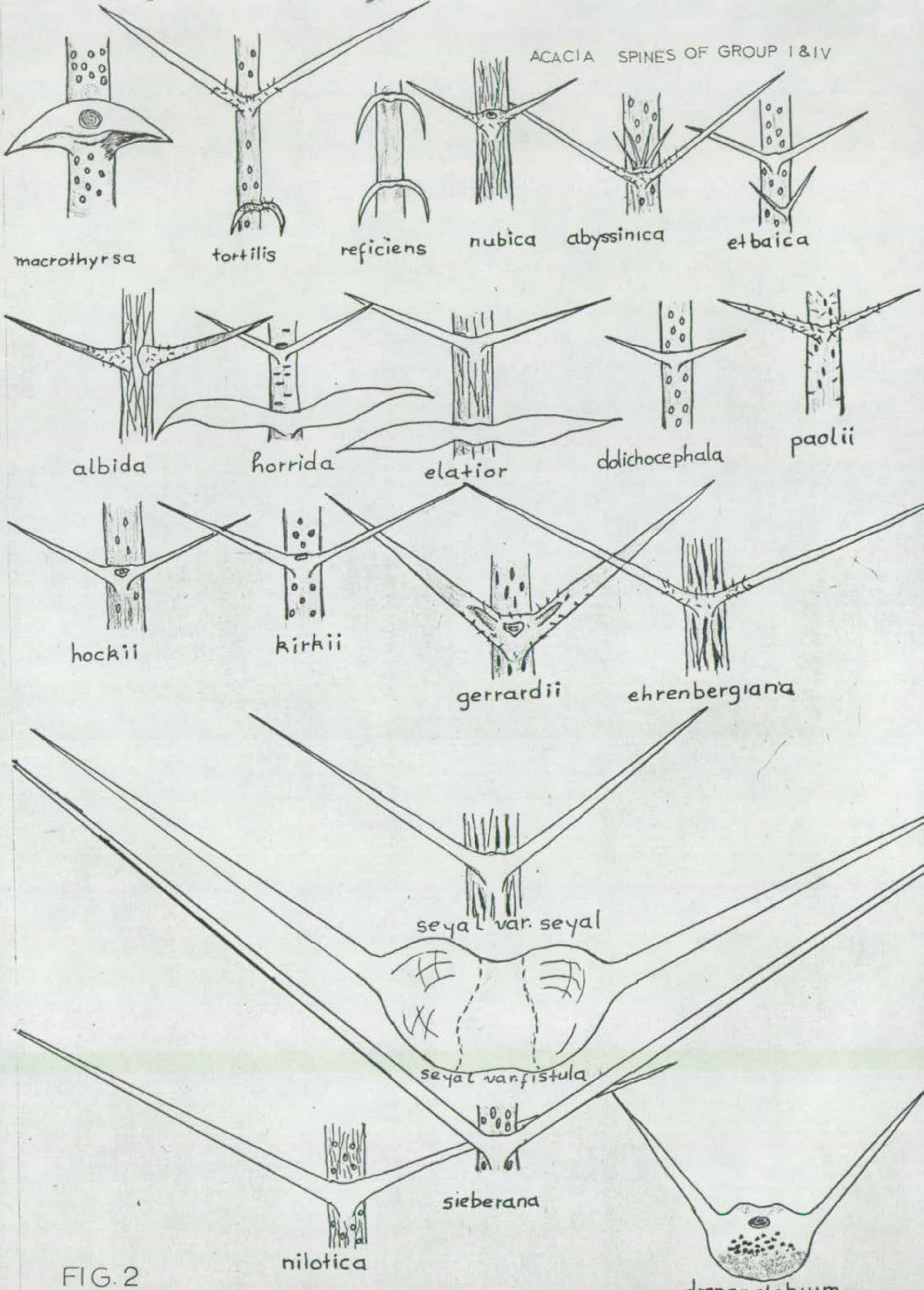

ACACIA SPINES OF GROUP I & IV
macrothyrsa
tortilis
reficiens
nubica
abyssinica
etbaica
albida
horrida
elatior
dolichocephala
paolii
hockii
kirkii
gerrardii
ehrenbergiana
seyal var. seyal
seyal var. fistula
sieberana
nilotica

FIG. 2

ACACIA PRICKLES (XI)

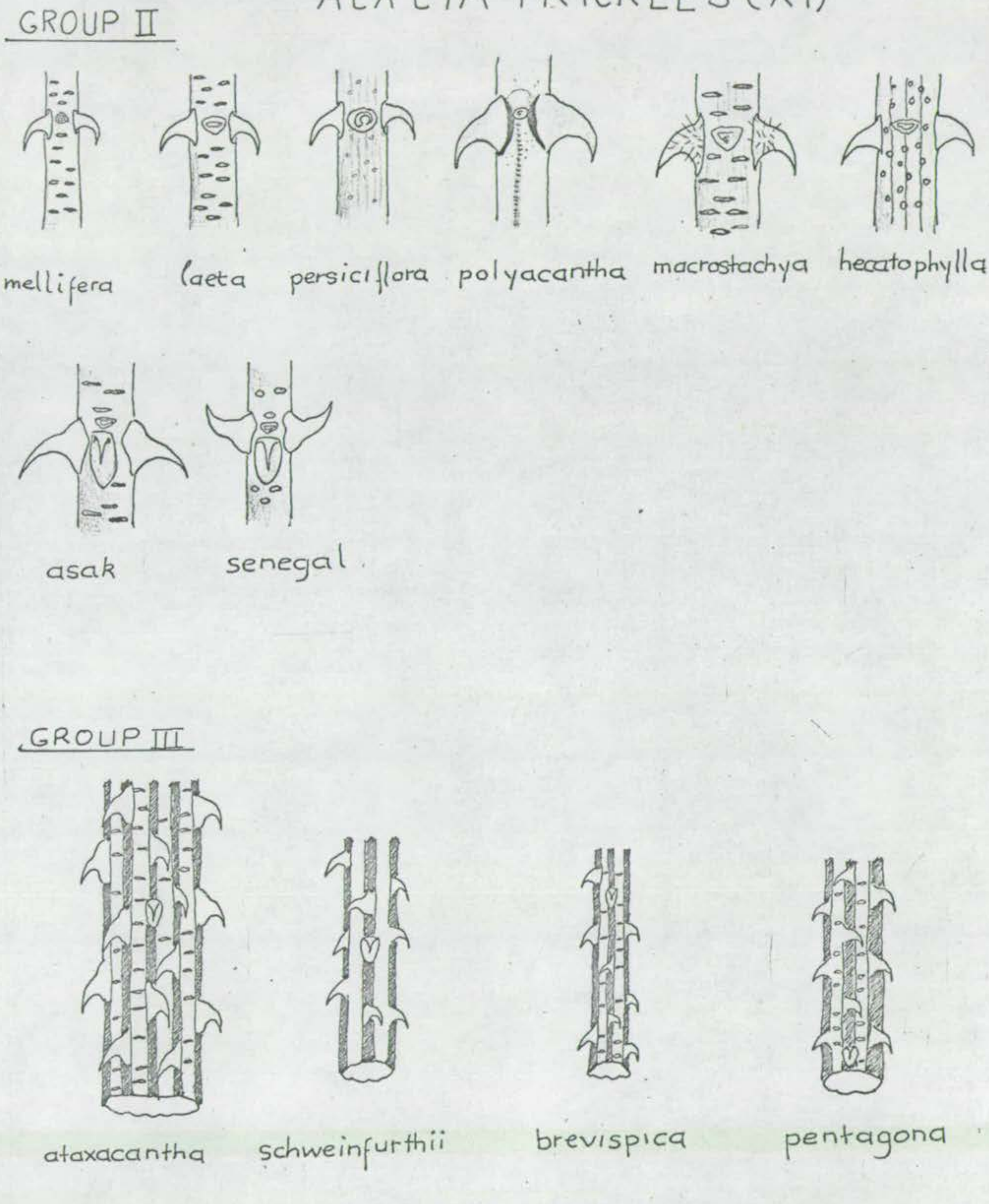


FIG. 3

occurred irrespective of the type of the inflorescence but showed an affinity to Groups II and III (non-spinescent stipules) and Groups I and IV (spinescent stipules). This correlation is true, according to my knowledge, not only in the Sudan species but in all the African species.

Amongst the Sudan species there are three species with the peculiar type of stipular spines in Group I, namely A. tortilis group, A. reficiens subsp. misera and A. macrothyrsa. In the first one there exists two types of spines on the same tree and even the same branch, with normal acicular, straight, white spines, together with hooked spines, slightly different in form from the falcate prickles; the hooked spines also occur exclusively in A. reficiens subsp. misera. In A. macrothyrsa the spines are grey and not acicular, with flat adaxial surface. Though these peculiar types of spines are different from the ordinary ones, they agree in the major feature of being stipular and having a vascular system.

A feature which is worth mentioning is the appearance of small yellow prickles on the rachis and rachilla on some of the prickled groups. These prickles are common on the rachis of all the climbers (Group III) in between every pair of pinnae. Some species of Group II may have prickles on the rachis, but the number of the prickles is very few (1-4), as in A. polyacantha subsp. camylacantha, A. macrostachya, A. hecatophylla and very few prickles in A. laeta and A. senegal, but this character is not at all consistent. Another feature, and almost in the same degree, is the occurrance of a few prickles, sometimes on the internodes, of A. polyacantha subsp. campylacantha, A. macrostachya and A. hecatophylla. This feature reflects some affinity between Groups II and III and suggests that one group may be derived from the other. In Group I this feature is completely absent.

Another important feature is that the two spicate species, A. horrida and A. albida, have spinescent stipules, but the length of the spines is comparatively shorter than the capitate species like A. nilotica and A. ehrenbergiana. A. lahai from South Africa has the same type of inflorescence as A. horrida and A. albida and it too has short spines.

5. Leaves (excluding stipules)

Sudan and African Acacias have bipinnate leaves, unlike the Australian Acacias where most of the Acacias have phyllodes or phylloclades. The Sudan Acacias have leaves with pulvinus,, a petiole and a rachis along which are borne a number of pairs of pinnae, giving in turn bearing pairs of small leaflets. The arrangement on the branches is alternate.

Glands: These occur on the petiole and on the rachis in between the pinnae pairs in almost all the species except A. albida where there are no petiolar glands, instead they are situated at the junction of each pinnae pair. These glands are variable in shape and colour in the different species.

Length: The leaf length varies from 2 cm in A. ehrenbergiana, 10 cm in A. seyal and A. gerrardi, to 90 cm in A. macrothyrsa. The variation in length is evidently correlated with the habitat, resulting in the smallest lengths in the arid zone, intermediate in the savanna zone and highest in the tropical southern zone.

Pinnae: The pinnae pairs are very few in the northern arid species. In A. ehrenbergiana in the desert regions, there may be one pair of pinnae and a maximum of three pairs; in A. tortilis, also in the desert to semi-desert regions, the pinnae pairs vary from 2 to 5. In Central Sudan, the dry savanna region, we get an average of 6-10 pairs, as in A. seyal and A. nubica. In the tropical southern regions the pinnae pairs vary from

10-40 as in A. abyssinica and A. polyacantha subsp. campylacantha. Thus the morpho-ecological correlation is, as expected, the drier the zone the less the number of pinnae pairs in the species. The same correlation holds well in the lengths of pinnae or rachilla. Members of Group I have the northern-most distribution and consequently the lowest number of pinnae pairs occurs in this group, but some members of this group, namely A. macrothyrsa and A. abyssinica, which grow in the tropical south, have the highest number of pinnae pairs. Group II members grow mostly in the tropical south and have a high number of pairs, while A. mellifera subsp. mellifera and A. laeta, which both grow in the central dry savanna zone, have the lowest number of pinnae pairs, being 2-3 paired. Group III, the climbers, has a high number of pinnae pairs and tropical habitats. A. albida is variable in its number of pinnae pairs and these follow the ecological changes.

Leaflets: The colour of the leaflets is normally dark to pale green, mostly oblong-lanceolate or sometimes obovate (A. mellifera and A. laeta). The length of the leaflet varies from 0.5 mm in A. tortilis to 8 mm in A. macrothyrsa, and a width ranging from 0.2 mm to 3 mm, and again the effect of the habitat is significant. The number of leaflet pairs is lowest in A. mellifera, being one pair, and highest in the southern species, being up to 60 pairs. The indumentum varies from glabrous to densely pubescent or puberulous; the margin can be ciliolate or not or partly ciliolate; the apex varies from acute, subacute, obtuse or round; the base is always obliquely cordate. The surface of the leaf is sometimes granular and the venation is not apparent except for the midrib. Few species have visible venation, e.g. A. mellifera and A. laeta. A noticeable phenomenon of the leaflets is the folding of the leaflet pairs in a "sleeping" position, like the Mimosa aspirata leaves, but in the Acacias leaf-folding is caused by darkness when the sun sets.

Rachis: The length of the rachis is comparable with that of the leaf length and the variation is ecologically correlated. The rachis is usually channelled or grooved adaxially. The indumentum is variable from glabrous to pubescent. Glands usually occur on the petiole and between the last 1-3 pinnae. It is noticeable also that the pulvinus is always bigger on longer leaves than shorter ones. In the short leaves of the north arid species the pulvinus is hardly seen.

Prickles: The leaves of the climbers (Group III) always have prickles along the rachis and sometimes the rachilla, which are apparently adaptations both for support on host trees and protection. A few, especially in Group II, sometimes have a few prickles along the rachis, while this feature is absent in Group I.

Generally the leaves of the Sudan Acacias are homogenous in shape except those of A. mellifera and A. laeta, which form a group which have other relatives in Africa. The length of the leaf in A. macrothyrsa is peculiar and considered as the largest amongst the Acacias. The leaves of A. abyssinica are also distinct in having very close-set pinnae and leaflet pairs, which raises their pair number to the highest level in the Acacias.

6. Inflorescence

There are two main types of inflorescences in the Acacias, cylindrical spikes (spicate) and globose heads (capitate), in addition to an intermediate stage between the two, found in A. dolichocephala, which is subglobose (ellipsoid heads). A. mellifera subsp. detinens of South Africa also has this sub-globose type. I have found one specimen of A. mellifera subsp. mellifera from the Sudan with the most peculiar type of inflorescence, where the normal type of spicate inflorescence has one "peduncle" with flowers arranged in a capitulum, (see Pl. 3 page 46). Another peculiar feature is found in A. dolichocephala, A. nilotica, A. seyal and A. hockii, where the involucel bears two or three flowers.

The peduncle of the spicate species has no bract and the flowers usually lie along the inflorescence either sessile or pedicellate as in A. mellifera, A. laeta, A. albida and A. ataxacantha. The length of the inflorescence is variable but tends to shorten in drier areas. The capitate species have an involucral bract lying along the peduncle; the position of the involucel is constant and in certain species characteristic. The capitate climbers have 2 pubescent bracts below the peduncles. In the capitulum the flowers arise from a floral bracteole which is spoon-shaped and very small.

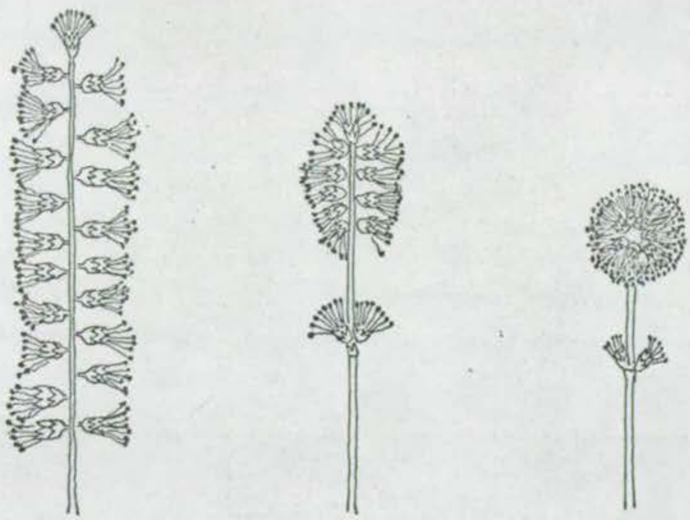
It is noticed that most of the species of the arid zone in Northern Sudan have a capitate inflorescence and in the tropical south spicate species predominate. In Central Sudan, in the savanna zone, a mixture of capitate and spicate species occur. A. albida is exceptional in being found all over the country. (See fig. 4A page 45).

7. Flowers

Colour: The usual colour of the Acacia flowers is creamy-white or yellow. There are three exceptions, A. macrothyrsa has deep orange colour and A. persiciflora and A. kirkii have red or pinkish corollas.

Size: The flowers are usually very small. The length of the flowers

A. INFLORESCENCE TYPES:



B. FLOWER TYPES:

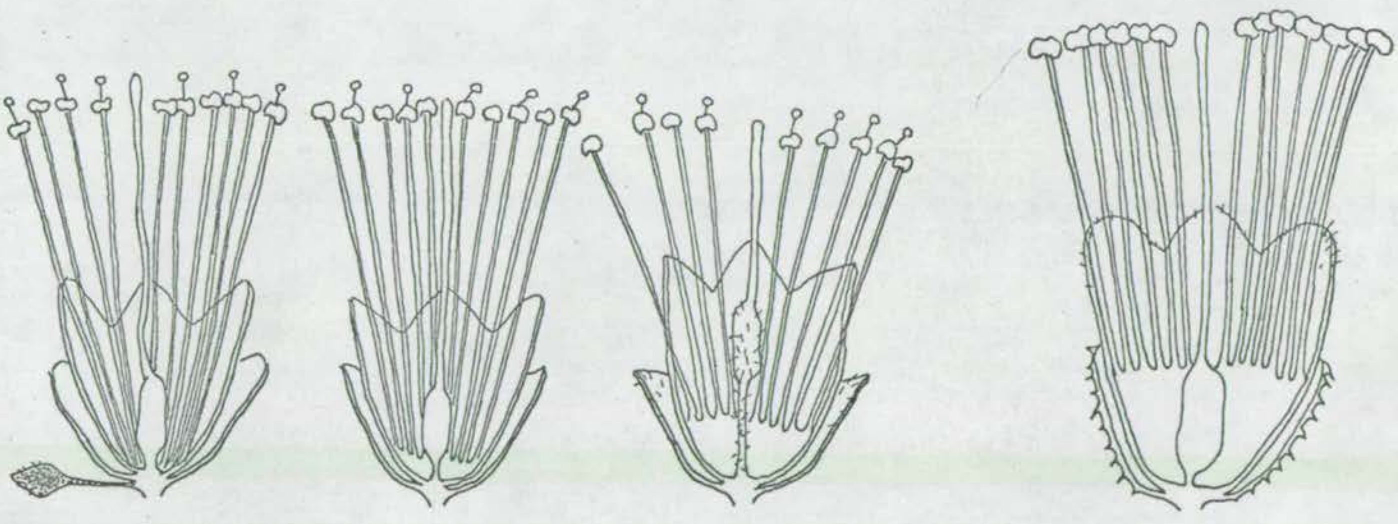


FIG.4

Plate 3. a. A. mellifera subsp. mellifera (x 2). Inflorescence of specimen No. 1489 showing a spicate inflorescence with 'peduncles' bearing flowers arranged in a capitulum.

b. A. nubica (x 275) T.S. through seed testa showing the structure of the areole.

a

b

Pl. 3

varies from 3.8 mm to 9 mm. A. albida has the longest flowers, which are 10 mm.

Calyx and corolla: They are both campanulate. The normal number of lobes is 5, but the species with capitate inflorescence occasionally have 4-7 lobes, as in A. nubica, A. gerrardii, A. abyssinica, A. sieberana, A. drepanolobium, A. tortilis, A. ehrenbergiana, A. seyal var. fistula, A. nilotica, all of them in Group I. The other groups, II, III and IV, have the normal number of 5 lobes in both series. The lobes are normally united, glabrous to pubescent.

Androecium: The stamens are many and free in Group I, united at the base in Group III, less united in Group II and united above the ovary length in A. albida. The stamens have a stipitate gland at the junction of the anther sacs and this exudes a sticky liquid to which the pollen becomes attached. Again A. albida is exceptional in not having these stipitate glands. The anther sacs vary in size, being largest in A. albida, large in Group I, small in Group II and smallest in Group III.

The gynoecium is superior in all Acacias. It is brown and oblong. The ovary is sessile in Group I, but in the other groups has a stipe (gynophore). In Group III the stipe is extremely long, longer than the ovary, and is hairy, a distinct character which separates the climbers from the rest of the Acacias (see fig.4B page45). The indumentum of the ovary is variable, but usually glabrous in Group I and pubescent in different degrees in the other groups. The style is filiform.

The Acacia flowers are actinomorphic, scented and insect-pollinated. An important feature which is apparent in this study is the presence of male flowers together with hermaphrodite flowers in Group I only, e.g. in A. nubica, A. abyssinica, A. tortilis, and A. nilotica, a feature absent in the other groups and may be a specialisation character in Group I. The sessile flowers, ovary, different number of floral lobes, and free stamens, are other characteristics of this group. A. albida has definite united eglandular stamens which separates it from the other Acacias in the flower characters. Groups II and III are related in floral characteristics but separated easily by the long hairy stipe (gynophore) of Group III. (Fig. 4B page 45).

8. Legumes

The legume or pod characters are very important in the genus and come next to the stipules. Their shapes, sizes, venation, colour, margins, indumentum, are extremely variable and can sometimes be utilised in separating species, but there is a uniformity of characters within the groups. The Sudan Acacias have dehiscent pods except for two species, A. albida and A. sieberana, and are either coriaceous, or, in a few species, membranous.

Colour: The pods of Group II are dark brown or pinkish-brown. In the three species A. mellifera, A. laeta, and A. senegal they are straw-coloured to light brown. Group III, the climbers, have brown to pinkish colour, like Group II members. In Group I the pods are yellow, pink or light brown. A. albida has an orange colour, which is distinct from all the other Acacias.

Ecologically there is a tendency for light and pale colour of pods to occur in the dry areas and darker colours in the tropical parts.

Size: The longest pods are found amongst the northern species of Group I where they reach up to 22 cm long; the other groups are smaller, ranging up to 10 cm long. There is a reduction of width as the pods get longer. The longest pods of Group I, found in the arid northern regions, have a small width of 0.4-1.5 cm; Group II members have a larger width of 2-3 cm. An ecological correlation with the pod size is evident; long and narrow in arid areas and shorter and broader in the tropical areas. This is also confirmed by a few members of Group I which are in the tropical parts and have short and wide pods, e.g. A. sieberana, A. macrothyrsa and A. nilotica subsp. subalata.

Shape: The Acacia pods are shaped into straight pods with an entire margin and few undulations, or else falcate and spiral pods with constricted margins. Group I has very few species with straight and non-constricted pods, e.g. A. abyssinica, A. elatior, A. reficiens, and these are all in the tropical southern areas; the majority of the group's pods are falcate constricted, e.g. A. seyal, A. drepanolobium, A. gerrardii and A. ehrenbergiana, and one species and its subspecies have developed spiral constricted pods, A. tortilis, which grows in arid areas. A. albida has peculiar pods in between falcate and coiled. The other two groups (II and III) have related pods, being straight with entire margins. No constrictions between the seeds exist in these two groups, but a few lobes or undulations occur occasionally, as in A. mellifera and A. senegal (see figs. 7 page 45) and both exist in Central Sudan. A good example to show the correlation of habitat and pod shapes is represented by the four subspecies of A. nilotica; subsp. subalata grows in the tropical parts and has a straight, non-constricted pod; subsp. astringens, growing in central western parts, has straight to falcate pods with indented margins; subsp. nilotica and tomentosa have falcate necklaced constricted pods, and they both exist in the northern parts of the Sudan. Thus a definite trend is established to have falcate or spiral constricted pods on the arid northern parts and straight non-constricted pods on the tropical parts. The Central Sudan is intermediate and it contains both types of pods. (See figs.5-8 pages 51-54).

Another correlated feature is the pod thickness. Groups II and III without exception have compressed or flattened pods, while Group I has non-compressed or non-flattened pods. This is also correlated with the compressed seeds of Groups II and III and non-compressed seeds of Group I.

Venation: All members of Groups II and III have the venation on the outer surface horizontal, a character which is strongly correlated with the stipular type. On the other hand, in Group I and *A. albida*, the venation is longitudinal, oblique or not apparent. In *A. kirkii* subsp. *mildbraedii* the veins converge radially to a central point on the pods and is considered here as oblique. In *A. nilotica*, *A. sieberana*, and *A. albida*, the venation is sometimes not apparent but few longitudinal ridges appear with some longitudinal veins (see fig. 6 page 52).

Position of seeds inside pods: The seeds inside the pods are held longitudinally, obliquely or horizontally by the funicle. The position at which the seeds lie is directly correlated with the width of the pods. If a pod is wide (Groups II and III) then it follows that there is enough space for the seed to be held horizontally inside the pod, while in Group I, where the pods are mostly narrow, the seeds are held longitudinally inside the pods. In a few species, e.g. *A. nubica*, *A. macrothyrsa* and *A. polyacantha* subsp. *campylacantha*, the width is intermediate and the seeds are held obliquely inside the pods (see fig. 8 page 54).

FIG. 5 ACACIA PODS (GROUP I) A

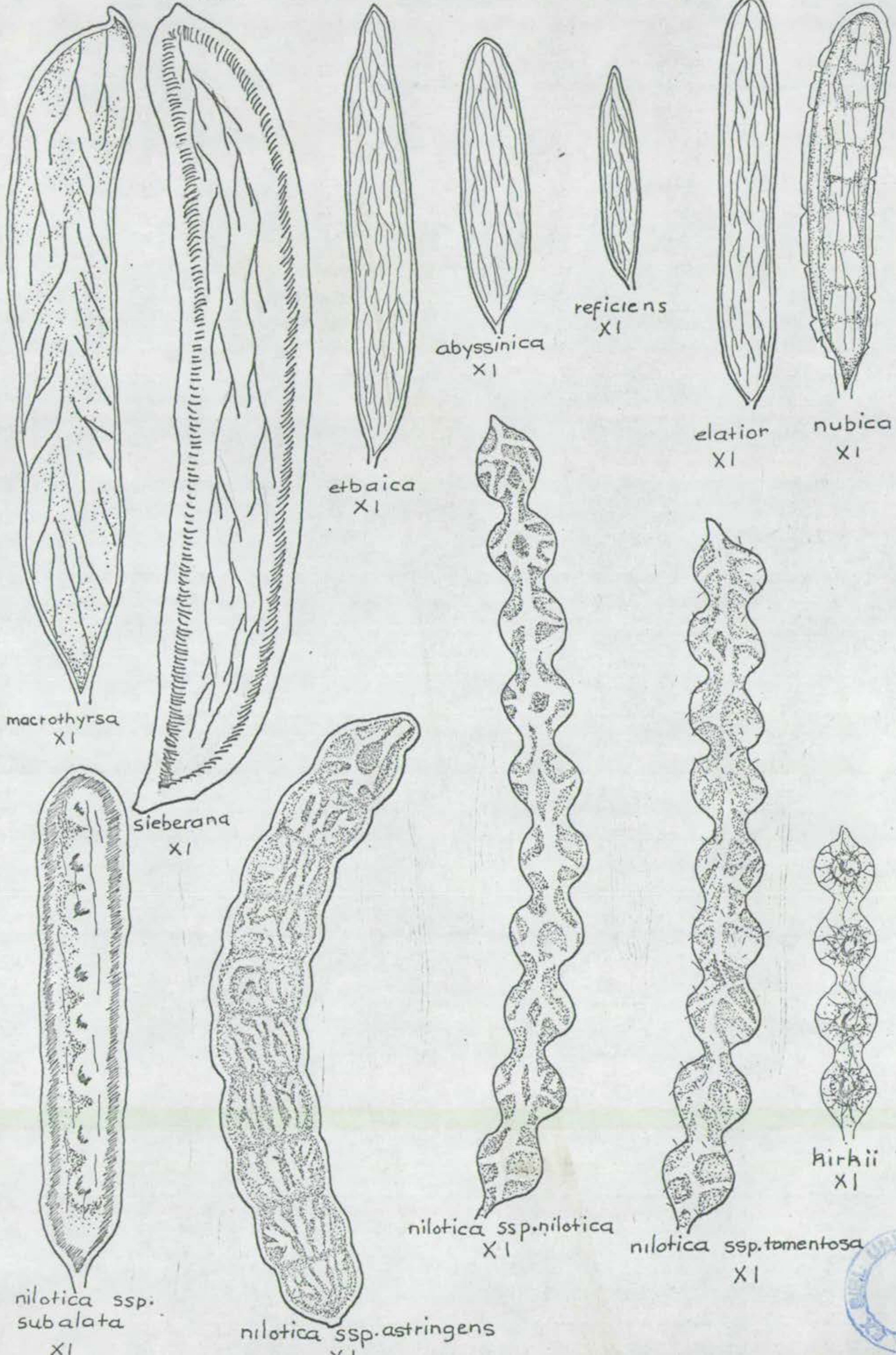


FIG. 6 ACACIA PODS (GROUP I) **B**

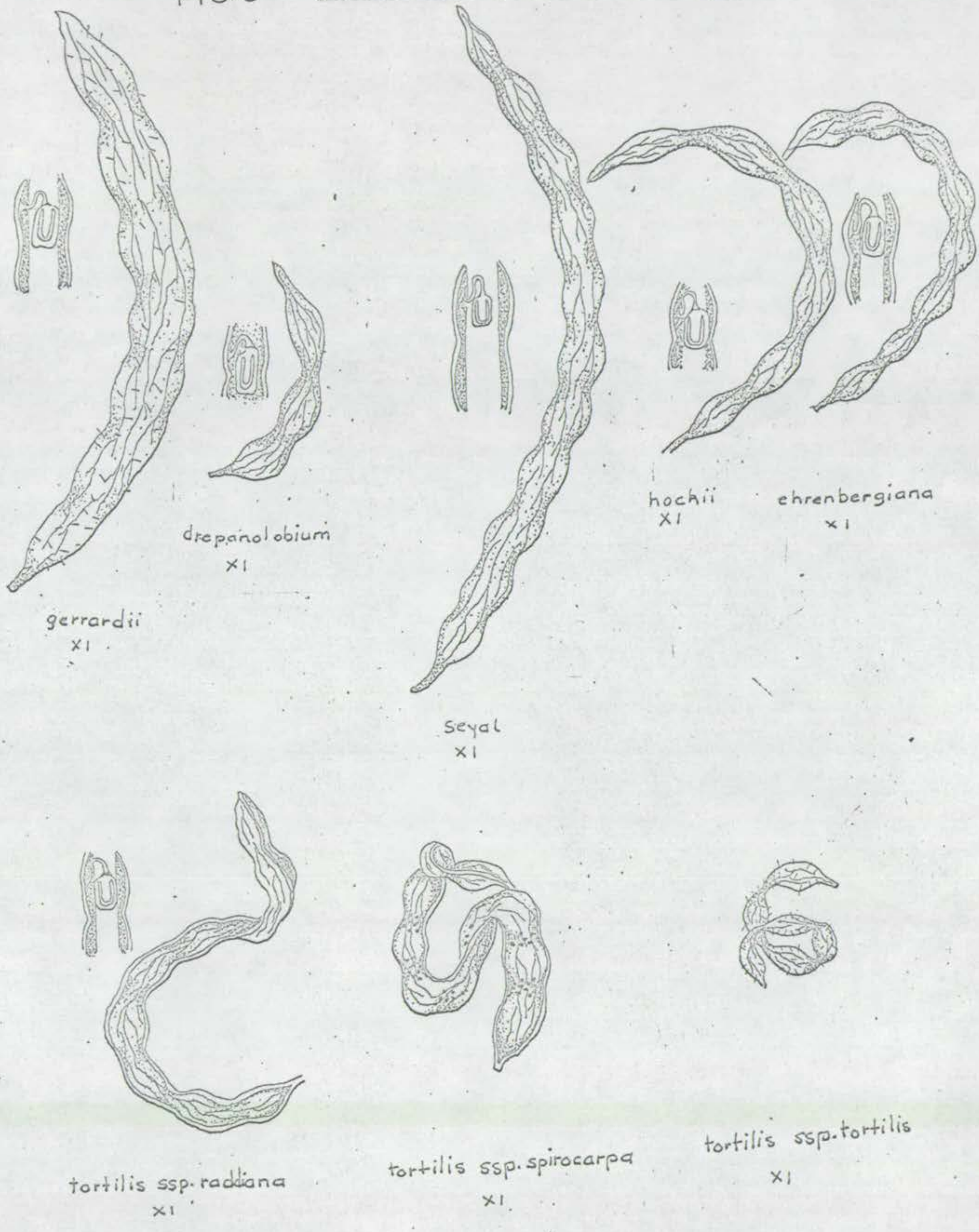


FIG. 7 ACACIA PODS (GROUP II)

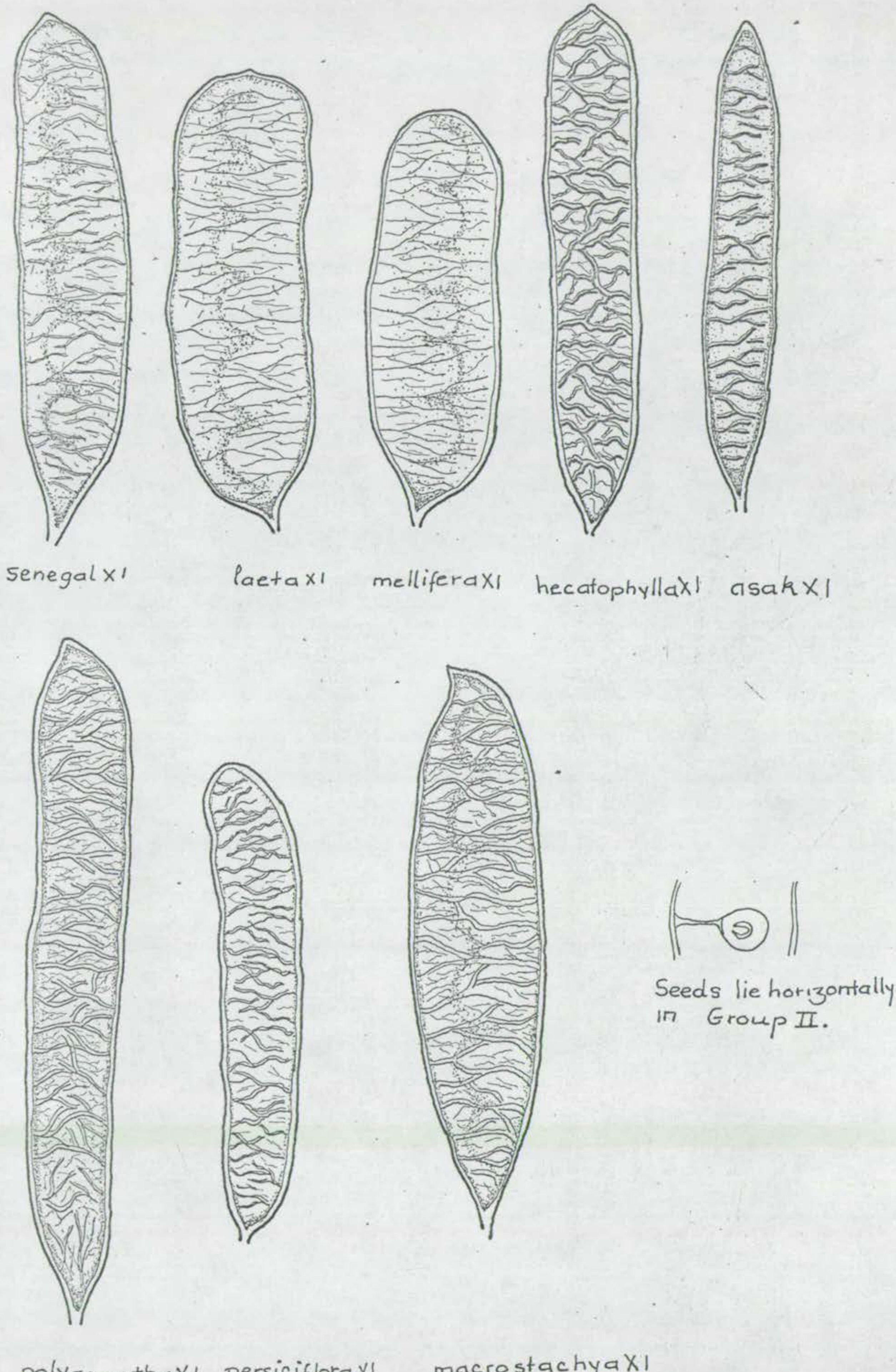
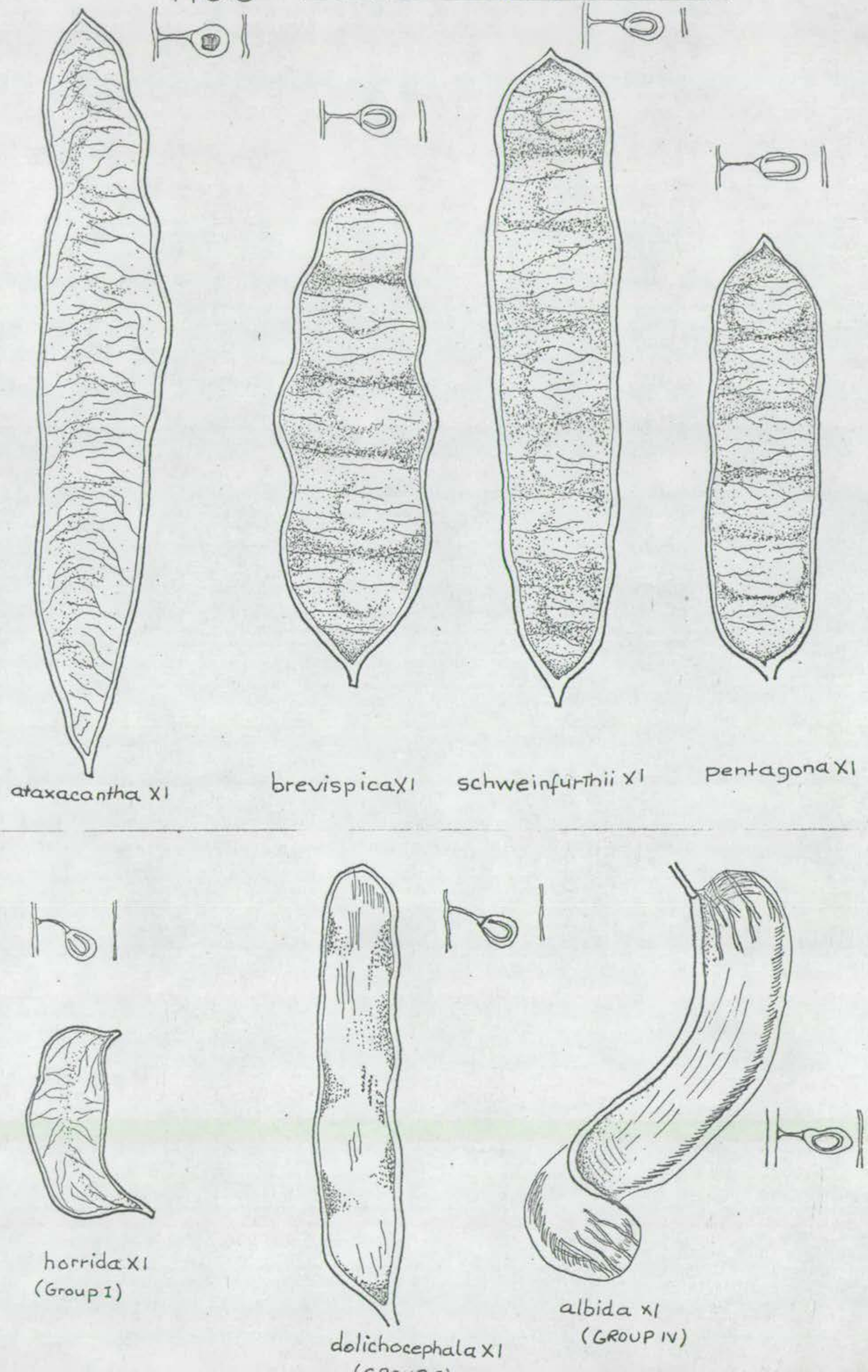


FIG.8 ACACIA PODS (GROUP III)



9. <u>Seeds</u>

The Acacia seeds show group uniformity of characters in many of their features. The colour of the seeds tends to be darker in the two Groups II and III and lighter in Group I, a character which also correlates with pod colour.

<u>Shape and size</u>: The species in Group I have oblong or elliptic seeds, while those in Group II all have circular or orbicular seeds. Group III contains a mixture of circular (<u>A. ataxacantha</u>) and slightly obovate and elliptic seeds, as in <u>A. brevispica</u> and <u>A. schweinfurthii</u>; in <u>A. pentagona</u> it is oblong. <u>A. albida</u> has obovate to elliptic seeds. <u>A. horrida</u> in Group I, which has spinescent stipules but spicate inflorescence, still has the oblong type of seed typical of Group I (see fig. 9 page 57).

There is a trend in seed thickness: all the circular seeds in Group II are compressed or flat seeds, while the thickness increases in Group III and reaches its maximum in Group I (e.g. <u>A. nubica</u>, <u>A. nilotica</u> and <u>A. sieberana</u>).

The length and width of the seeds show the same correlations, being shortest in Groups II and III and longest in Group I. In these characters <u>A. albida</u> has more affinity with Group I than the other groups.

<u>Funicle</u>: It is noticeable that species with seeds arranged horizontally in wider pods consequently have a shorter funicle (e.g. <u>A. mellifera</u> and <u>A. macrostachya</u>) than those with seeds lying longitudinally in narrow pods, because of the longer distance the funicle has to coil itself in the longitudinal position of seeds. The colour of the funicle is also lighter in narrow pods and darker in wider pods.

<u>Areole</u>: The form of the areole is an important character in the Acacia

seeds. Anatomically it is a fissured area on the surface of the testa where the epidermis and the paliside layers are removed from both surfaces of the seeds, resulting in continuous lines which lie central in the shape of a crescent or marginal in a U or O-shape (see Pl.3b page 46). The function of this areole is not definitely known but it is possibly an area for the absorption of water during germination.

There are three types of areoles appearing in the Acacia seeds as follows:

1. Crescent-shaped areole: The fissuring is always in the shape of a crescent and always lies on the centre of seeds which are necessarily circular or orbicular. It is found in all members of Group II and one member of Group III, namely _A. ataxacantha_.
2. U-shaped areole: The fissuring is in the shape of a U and is always near the margin of the side. The opening of the U faces the micropyle. The length of the U follows the length of the seed. This feature is found in Group I and the capitate species of Group III, namely _A. brevispica_, _A. schweinfurthii_ and _A. pentagona_.
3. O-shaped areole: This is also a feature of Group I where the areole is in the shape of O, i.e. the arms are closed, and is near the margin of the seeds. This type of O-shaped areole is found in _A. nilotica_, _A. sieberana_ and _A. nubica_. _A. albida_ has both O and U-shaped areoles.

At a first look it seems that there is a correlation between the areole shape and the inflorescence types, but this correlation is distorted by _A. horrida_ and _A. albida_, both having marginal U-shaped areoles (see fig. 9 page 57).

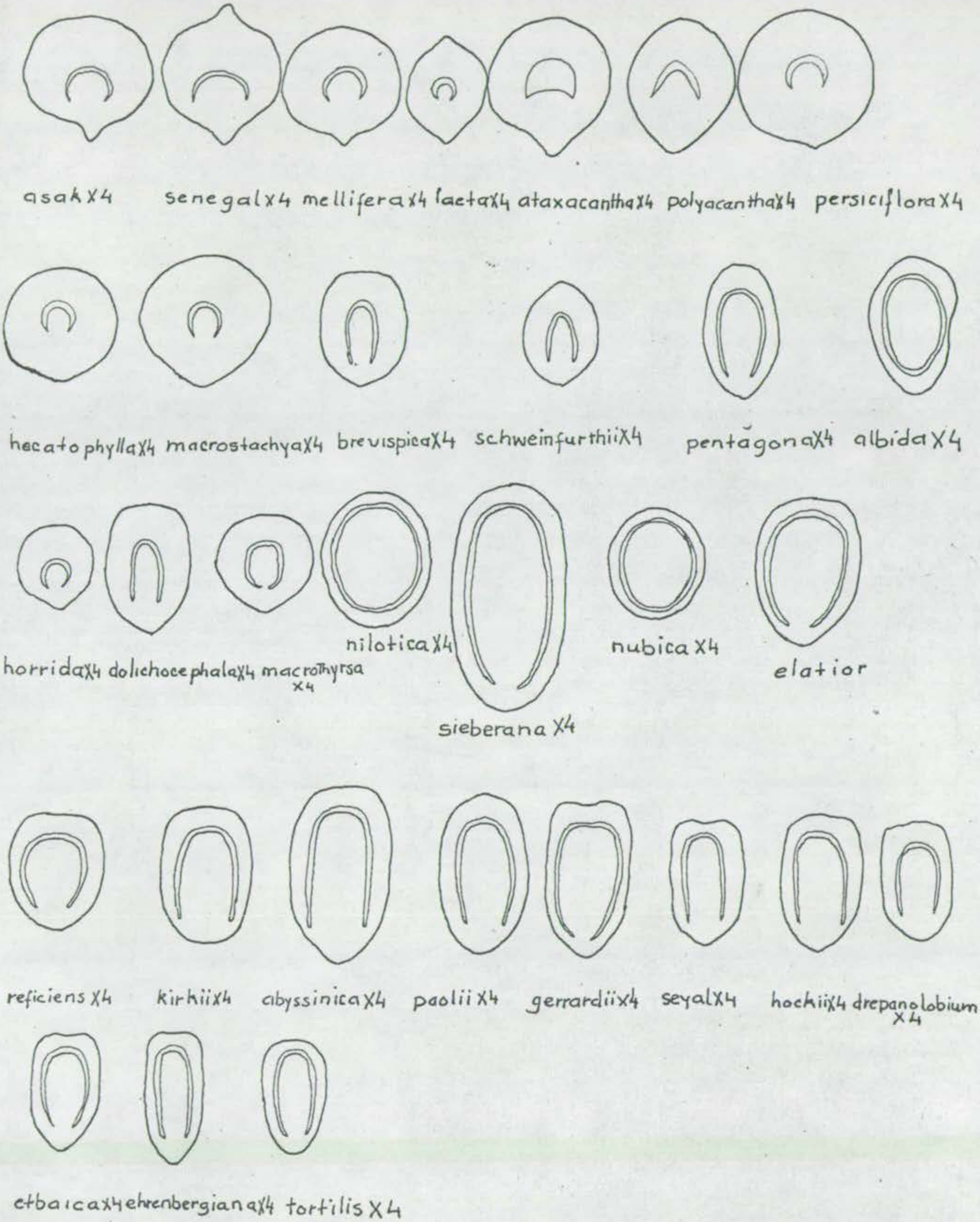


FIG.9 SEED SHAPES & AREOLES

To summarise the above, the Groups have the following fruit and seed characters:

GROUP I:

Pods light brown, yellow or pink, 22 x 0.4-1.5 cm, few straight with entire margin, mostly falcate to spiral and constricted margins, non-compressed; venation longitudinal, oblique or not apparent. Seeds lie longitudinally, occasionally obliquely. Seeds light colour, oblong or elliptic, not compressed; funicle long, pale colour; areole O-shaped, marginal.

GROUP II:

Pods dark brown, pink, 10 x 2-3 cm, straight, entire margin or rarely lobed, no constrictions on margin, compressed; venation horizontal. Seeds lie horizontally, dark colour, circular, compressed; funicle short, dark colour; areole crescent-shaped, central.

GROUP III:

Pods dark brown, pink, 10 x 2-3 cm, straight, entire margin, not constricted, compressed; venation horizontal. Seeds lie horizontally, dark colour, circular (*A. ataxacantha*) mostly oblong, not compressed; funicle short, dark brown; areole crescent-shaped, central to O and U-shaped, marginal.

GROUP IV: *A. albida*

Pods orange, not compressed, length and width intermediate, coiled to falcate; margin entire, not constricted; venation longitudinal or not apparent. Seeds lie horizontally, brown colour, obovate to oblong, not compressed; funicle short, dark brown; areole O and U-shaped, marginal.

B. SEEDLING DEVELOPMENT

Materials and methods

The Acacia seeds prepared for germination studies were collected in the field from Sudan. Large healthy seeds without insect holes were chosen. Before germination two pre-treatments were carried out:

1. Seeds were pre-treated in concentrated sulphuric acid for one hour and left to dry. They were then soaked in warm water for 24 hours.
2. The testa of the seeds was then cut at a point away from the micropylar end to make a small slit to allow water to go into the cotyledons. They were then soaked in warm water for 24 hours.

The above treatments are essential, because the testa is extremely hard and impermeable.

Five treated seeds of every species were then put on moist filter paper placed over glass slides, which were resting at an angle on the rim of a petriglass dish. They were put at a temperature of 23°C and watered daily with warm water.

Another method of germination was to put the treated seeds in soil compost inside plastic or clay pots and leave them in a warm glasshouse at a temperature of 70°C. Germination by this method takes place after 24 hours, while using the water germination on petri dishes takes 24-48 hours, or slightly more with certain species.

Germination and seedlings development

Germination in the Acacias is epigeal. The embryo produces a stout radical below the soil level and the hypocotyl is the first part to appear above the soil level, carrying with it the cotyledons. It soon develops a main shoot giving the first leaves after the immediate opening of the two cotyledons. The hypocotyl is usually glabrous and green, but occasionally pink. It is terete in Groups I and II, angular in Group III, and grooved in A. albida (Group IV).

The cotyledons are green and fleshy; the shape of the lamina follows that of their seeds. The apex of the cotyledons is round and the base is sagittate with developed auricles. The cotyledons are usually convex above and flat below, being oblong, obovate-oblong or orbicular. When they first come out of the soil they stand vertically but after 2-5 days change into a horizontal position.

According to the results which I have obtained from these germination tests, the development of the first leaves on the stem is remarkably variable in Acacia and has important taxonomic significance. The first leaf appearing on the stem after the cotyledons is usually a pinnate leaf, followed by a second leaf which is bipinnate. Some workers who studied Australian species found that after the second bipinnate leaf was formed, the petiole is flattened to give phyllodic leaves which persist in the adult form of the trees. This indicates an evolutionary trend in the development of the Australian species, but the African Acacias have different modifications to the Australian trend of pinnate, bipinnate and phyllodic. The following developmental patterns appear in the Sudan Acacias studied in this work.

Pattern 1: First leaf pinnate; second leaf bipinnate and alternate; third leaf bipinnate and alternate.

Pattern 2: First and second leaf pinnate and opposite; third leaf bipinnate and alternate.

Pattern 3: (a) First leaf bipinnate (2 pinnae pairs); second leaf bipinnate (2 pinnae pairs and alternate; third leaf bipinnate (2 pinnae pairs) and alternate.

(b) First and second leaf bipinnate (2 pinnae pairs) and opposite; third leaf bipinnate (2 pinnae pairs).

(c) First leaf bipinnate (1 pinnae pair); second leaf bipinnate (1 pinnae pair) and alternate; third leaf bipinnate (2 pinnae pairs) and alternate (see fig. 10 page).

The following table shows these patterns appearing in the following investigated species: alt. = alternate; opp. = opposite; + = 1 pair of pinnae; ++ = 2 pairs of pinnae.

TABLE 2

Name of species	First leaf		Second leaf		Third leaf	
	pinnate	bi-pinnate	pinnate	bi-pinnate	pinnate	bi-pinnate
1. A. ehrenbergiana	+			+(alt.)		+(alt.)
2. A. gerrardii	+			+(alt.)		+(alt.)
3. A. sieberana	+			+(alt.)		+(alt.)
4. A. drepanolobium	+			+(alt.)		+(alt.)
5. A. nilotica subsp. tomentosa	+			+(alt.)		+(alt.)
6. A. nilotica subsp. nilotica	+			+(alt.)		+(alt.)
7. A. nilotica subsp. astringens	+			+(alt.)		+(alt.)
8. A. tortilis subsp. tortilis	+			+(alt.)		+(alt.)
9. A. tortilis subsp. raddiana	+			+(alt.)		+(alt.)

(Cont.) Name of species	First leaf pinnate	First leaf bi-pinnate	Second leaf pinnate	Second leaf bi-pinnate	Third leaf pinnate	Third leaf bi-pinnate
10. A. tortilis subsp. spirocarpa	+			+(alt.)		+(alt.)
11. A. seyal subsp. seyal	+			+(alt.)		+(alt.)
12. A. seyal subsp. fistula	+			+(alt.)		+(alt.)
13. A. horrida	+			+(alt.)		+(alt.)
14. A. elatior	+			+(alt.)		+(alt.)
15. A. hockii	+			+(alt.)		+(alt.)
16. A. kirkii	+			+(alt.)		+(alt.)
17. A. dolichocephala	+			++(alt.)		++(alt.)
18. A. nubica	+		+(opp.)			+(alt.)
19. A. paolii	+		+(opp.)			+(alt.)
20. A. abyssinica	+		+(opp.)			+(alt.)
21. A. farnesiana (American)	+		+(opp.)			+(alt.)
22. A. polyacantha ssp. campylacantha	+			+(alt.)		+(alt.)
23. A. senegal	+			+(alt.)		+(alt.)
24. A. laeta	+		+(opp.)			+(alt.)
25. A. mellifera	+		+(opp.)			+(alt.)
26. A. ataxacantha		++		++(alt.)		++(alt.)
27. A. brevispica		++		++(opp.)		++(alt.)
28. A. schweinfurthii		++		++(opp.)		++(alt.)

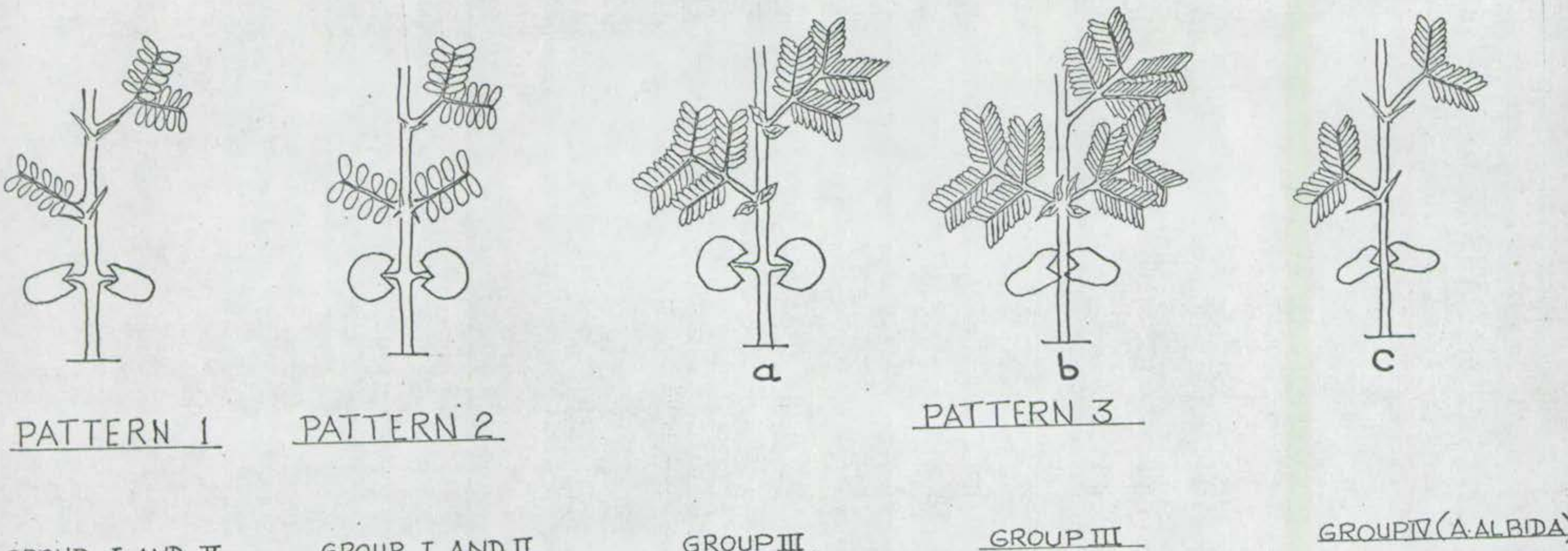


FIG.10 SEEDLING DEVELOPMENT.

(Cont.) Name of species	First leaf pinnate	First leaf bi-pinnate	Second leaf pinnate	Second leaf bi-pinnate	Third leaf pinnate	Third leaf bi-pinnate
29. A. kraussiana (S. Africa)		++		++(opp.)		++(alt.)
30. A. albida		+		+(alt.)		+(alt.)

As seen from the previous table, Group I (1-21) shows both the first and second patterns of seedling development; Group II (22-25) again has both patterns 1 and 2. Group III (25-29) has patterns 3(a) and (b); Group IV, A. albida (30) has pattern 3(c) which differs from that in Group III, in having 1 pair of pinnae instead of 2 pairs.

However, certain unusual patterns are characteristics of certain species and show the wide and remarkable variations in seedling development between individual species. The following is an outline of these characters in each of the studied species:

1. A. ehrenbergiana: Shares the same pattern of development of its Group I, with pinnate-bipinnate progression, but is peculiar in having a fast rate of growth (19 cm in 4 weeks) and in developing many nodes on the stem at short internodes. The first 2-pinnae paired leaf develops at the 10th node. The hypocotyl is terete, short, 1.5 cm long. The cotyledons are oblong and petiolate and are shed very early . Stipules spinescent.

2. A. gerrardii subsp. gerrardii: Pattern 1. The rate of growth is very slow (7 cm in 4 weeks) but a high number of leaflet pairs is produced. It is peculiar in having very dark green leaflets which separates it at first glance from the light green leaves of other Acacias. It develops its

2-paired pinnae leaf at the third node. Its hypocotyl is the shortest, being 0.8 cm. The cotyledons are oblong and petiolate. Stipules spinescent.

3. A. sieberana var. sieberana: Pattern 1. It has the tallest and stoutest seedling and a quick rate of growth (19 cm in 4 weeks). It has a high number of leaflet pairs in its first leaf (13 pairs). The first 2-paired pinnae leaf appears at the 5th node. The hypocotyl is the longest, 6 cm in 6 weeks. The cotyledons are also the largest in the genus, petiolate and persisting for a long period. This indicates a correlation of the seed size which is the largest in this species (10-12 x 7.5-9 mm) and the size of the seedling parts. Stipules spinescent.

4. A. drepanolobium: Pattern 1. A very slow species to develop (4 cm in 4 weeks). Its 2-paired pinnae leaf appears at the 5th node. The cotyledons are oblong and petiole. Stipules spinescent,

5. A. nilotica: Pattern 1. It is peculiar in having a pink colour on the root, hypocotyl and leaf. The 2-paired pinnae develops early at the 3rd node. In one case the second leaf had 2-paired pinnae. Cotyledons oblong and petiolate. The two subsp. nilotica and tomentosa behave similarly in the seedling stage, but subsp. astringens is different in not developing the pink colour. Stipules spinescent.

8. A. tortilis subsp. tortilis and spirocarpa: Pattern 1. Its rate of growth is rather slow (10 cm in 4 weeks), but its stem develops the highest number of nodes and is densely puberulous. The first leaf has a low number of leaflets, 5-paired. The hypocotyl grows 3.5 cm in 6 weeks and is densely puberulous. Cotyledons oblong, petiolate and are shed early. The 2-paired pinnae leaf developes at the 5th node. The seedling is peculiar in going

back to a 1-paired pinnae leaf, followed again by 2-paired pinnae leaves, and this sequence is repeated many times. Stipules spinescent.

9. A. tortilis subsp. raddiana: Pattern 1. Fast growing (20 cm in 4 weeks); hypocotyl 2.5 cm in 6 weeks. Unlike the above subspecies, the seedling is glabrous. The leaflets are also glabrous and bigger than in the other subspecies. The repetition of the 2-paired pinnae leaf to 1-paired pinnae leaf sequence also occurs here. Cotyledons oblong, petiolate and are not shed early. Its seedling characteristics are different from those of the other two subspecies which, in addition to other characters discussed in the next chapter, might lead one to question treating it as a separate species. Stipules spinescent.

11. A. seyal var. seyal: Pattern 1. The 2-paired pinnae leaf appears at the 5th node and has characteristically long internodes and consequently fewer leaves. The hypocotyl is short (2 cm in 4 weeks) and the cotyledons are oblong, petiolate and are shed early. Stipules spinescent.

12. A. seyal var. fistula: As var. seyal, but slightly slower in growth. It keeps its cotyledons for a long period. Stipules spinescent.

13. A. horrida: Pattern 1. The cotyledons are oblong and petiolate. A peculiar feature is the appearance of secondary leaves in the axil of the primary leaves at the third week. Stipules spinescent.

14. A. elatior: Pattern 1. Cotyledons oblong and petiolate. Stipules spinescent.

15. A. hockii: Pattern 1. Cotyledons oblong and petiolate. It produces 2-3 hypocotyls, each shoot repeating the same pattern 1. Stipules spinescent.

16. A. kirkii: Pattern 1. Cotyledons oblong and petiolate.

17. A. dolichocephala: Pattern 1. Cotyledons oblong and petiolate. The second leaf which is bipinnate, has 2 pairs of pinnae (this feature appears occasionally in A. nilotica). Again like A. nilotica it has a pink hypocotyl and like A. horrida it produces secondary leaves in the axil of the primary leaves after 3 weeks. Stipules spinescent.

The following species, though of the same Group I, have Pattern 2 of seedling development:

18. A. nubica: Pattern 2. Two opposite pinnate leaves followed by alternate bipinnate leaves. It is the quickest species to germinate and the one with the highest number of viable seeds. Cotyledons are oblong and petiolate. The 2-paired pinnae leaf appears at the 6th node. Stipules spinescent.

19. A. paolii: Pattern 2. The 2-paired pinnae leaf appears at the third node. The cotyledons are oblong and petiolate. The seedling is densely pubescent and grows quickly (20 cm in 4 weeks). Stipules spinescent.

20. A. abyssinica: Pattern 2. The cotyledons are oblong and petiolate. The 2-paired pinnae leaf first appears at the 6th node, after which successive leaves multiply quickly in number of pinnae and leaflet pairs. The leaflet size is noticed to decrease in size with increase of their number. Stipules spinescent.

21. A. farnesiana: (Native to Central America and introduced to the Sudan). It has spinescent stipules and a capitate inflorescence and thus belongs to Group I. Pattern 2. The third bipinnate leaf is sometimes distorted with irregular pinnae patterns and the leaflets occasionally fuse to form one simple leaf. The cotyledons are oblong and petiolate. Stipules spinescent.

The above 21 species and subspecies of Group I all agree in having petiolate oblong cotyledons. Spines also appear at the nodes in pairs; these are actually stipules which are modified into spines which appear in the seedling as short acicular structures that soon harden into persistent spines.

The following four species are members of Group II which agree with Group I in having the same patterns 1 and 2, but differ in cotyledons and stipules characters:

22. A. polyacantha subsp. campylacantha: Pattern 1. The cotyledons are petiolate but their shape is orbicular and they remain on the seedling for a long time (6 weeks). The 2-paired pinnae leaves appear at the 5th node. The hypocotyl reaches 4 cm in 4 weeks. A pair of scale-like stipules which are membranacous and filiform appears at the nodes and under them a pair of colourless falcate prickles appears after 3 weeks. Hypocotyl terete.

23. A. senegal: Pattern 2. Same as above but slightly slower in growth. Hypocotyl is 1.5 cm in 4 weeks. The cotyledons are again circular or orbicular and petiolate. Two scale-like stipules arise at the nodes and after 3 weeks three prickles appear under the stipules; these prickles are falcate, colourless or whitish-yellow. Hypocotyl terete.

The following species in Group II have Pattern 2 as in A. nubica, A. abyssinica, A. paolii and A. farnesiana:

24. A. laeta: Pattern 2. The two opposite pinnate leaves have 4 pairs of big obovate leaflets. The third leaf is bipinnate with 2 pairs of pinnae and 3 pairs of leaflets. . The cotyledons are orbicular and petiolate. The stipules

are present as scale-like structures on the nodes. After 3 weeks a pair of falcate, yellow or colourless prickles appears under the stipules.

25. A. mellifera: Pattern 2. Same as A. laeta, except that the third leaf has 2 pairs of pinnae and one pair of obovate leaflets which persist in the adult stage. Hypocotyl terete.

Thus Group II agrees with Group I in having both patterns 1 and 2, but differs sharply in the characters of the cotyledons and stipules.

The following 4 species are all climbers and belong to Group III. A. kraussiana is from South Africa and is studied here to confirm the climbers pattern in other parts of Africa:

26. A. ataxacantha: Pattern 3(a). First, second and third leaves are bipinnate (2 pairs of pinnae) and alternate. The fourth leaf has 3 pairs of pinnae, and the number of pinnae and leaflets hence increases steadily. The cotyledons are orbicular and are petiolate. The most prominant feature is the presence of stipules which are foliate with distinct dark green lamina with distinct reticulate venation. The prickles which are falcate appear on the internodes, rachis and rachilla. The hypocotyl is long - 4.5 cm in 4 weeks - and the cotyledons are shed in 2 weeks' time. The hypocotyl is also distinct in being angular. The petiolar gland is pink.

27. A. brevispica: Pattern 3 (b), but in one specimen the first and second leaves were almost alternate. The other characters as above, except that the cotyledons are obovate and sessile to subsessile. Petiolar gland pink.

28. A. schweinfurthii: Pattern 3(b). As above, but the cotyledons are definitely subsessile and obovate. Petiolar gland is pink.

29. A. kraussiana: Pattern 3(b). As above, but the seedling is densely pubescent.

The above 4 species of Group II differ sharply from Groups I and II in the type of seedling pattern by immediately developing bipinnate leaves. The cotyledons are a mixture of orbicular (A. ataxacantha) and obovate (A. brevispica and schweinfurthii); the cotyledons can also be petiolate, subsessile or sessile. The stipules are also different from the other groups in being foliate. The prickles which in Group II appear on the nodes in 2s or 3s, here in Group III appear scattered on the internodes, rachis and rachilla. The hypocotyl in Group III is angular as compared with the other two groups I and II, which are terete.

30. A. albida: Pattern 3(c). The first, second and third leaves which are bipinnate, have one pair of pinnae and are alternate. This 1-paired pinnae leaf is consistent up to the 10th node. The cotyledons are obovate and sessile. The stipules are spinescent acicular, which soon develope into hard persisting spines. The shoot soon acquires a white colour (unlike other Acacias) consisting of flaking pieces of bark. Secondary leaves appear after 4 weeks on the axils of the primary leaves. After the 10th node 2-paired pinnae leaves may appear, but again go back to producing 1-paired pinnae leaves. The cotyledons fall after 2 weeks. The seedling tends to have pendulous branches. Hypocotyl striate.

Thus, though A. albida is related to the climbers in having first leaves bipinnate, it differs sharply from the climbers by having 1 pair of pinnae and a terete hypocotyl, as compared with 2-paired pinnae and angular hypocotyl of the climbers.

Synopsis of seedling characters of the 4 groups

Group I: Pattern 1 and 2; stipules spinescent; cotyledons oblong and petiolate; hypocotyl terete.

Group II: Pattern 1 and 2; stipules scale-like; prickles present on nodes in twos or threes; cotyledons orbicular and petiolate; hypocotyl terete.

Group III: Pattern 3 (a) and (b); stipules foliate; prickles present on internodes, rachis and rachillae; cotyledons orbicular or obovate, petiolate or sessile; hypocotyl angular.

Group IV: Pattern 3 (c); stipules spinescent; cotyledons obovate and sessile; hypocotyl striate or grooved.

Discussion of the results

Before discussing the results of this study, it is appropriate to summarise the work in this field by previous workers.

Studies on the Acacia seedlings started in 1892 by J. Lubbock, who was working on Mimosaceae seedlings. He noticed the trend of pinnate, bipinnate and phyllodic sequence in the Australian Acacias. Another trend he noticed was 1st, 2nd and 3rd leaves all pinnate and then the fourth phyllodic.

Cambage (1915-28) worked on the Australian and American species and observed the sequence of pinnate, bipinnate and phyllodic in the Australian Acacias and all bipinnate leaves in the two American species he had studied. He came to the conclusion that the pinnate form is the ancestral type and the bipinnate and phyllodic are advanced types.

Vassal (1963-65) worked on Acacias of the Old and New Worlds and arrived at 3 modes of seedling development corresponding to the 3 patterns in this study, but he used Bentham's classification of the genus and the interpretation was difficult. He could not separate the non-spinescent stipulate

Acacias of Group II in this work from the climbers (Group III) because Bentham had combined them under one series, the Vulgares. Vassal treated A. albida as Bentham did, i.e. belonging to series Gummiferae, but due to its peculiar seedling development he proposed separating A. albida from the Acacias and putting it in the monotypic genus Faidherbia under the Ingeae. (This treatment had been proposed before by Chevalier 1934.)

Most recently, and at the same time as this study, a paper appeared on seedling development of South African and Australian Acacias by Robbertse & Schijff (1971); they observed 10 types of seedling development which are the same as my findings, but split the 3 patterns into 10 types. Their interpretation of the results is different from those in this paper; they used Bentham's classification and initiated a "suborder" Farinosae comprising some of the climbers (Group II) and A. albida (Group IV) due to the bipinnate trend of their seedling development, thus neglecting the important nature of the stipules in A. albida as compared with the climbers, and also the outline of the hypocotyl which is angular in the climbers and quite distinct from that of A. albida. There are many other characters which keep A. albida away from the climbers and even all the other Acacias. The two authors also recognised two major groups of seedlings based on the character of the cotyledons being sessile or petiolate. Sessile cotyledons appear in A. albida, two climbers and most of the Australian species according to the authors' observations, but these three groups of Acacias definitely cannot be included in one natural division. Robbertse and Schijff concluded their study with a phylogenetic hypothesis concerning the ancestral Acacia as having a diploid number of 26 chromosomes, spicate inflorescence, and seedlings with two or more pinnate or two bipinnate juvenile leaves and sessile cotyledons; from this hypothetical progenitor several different lines of development conceivably occurred.

In my study phylogenetic interpretation will be left to the end, after looking at all the investigated fields to achieve the maximum coordination of characters.

The present results from the Sudan species produced the three patterns already mentioned, together with the three corresponding developments of the stipules, which are frequently referred to in this work as the basis of the classification of the genus. The character of the cotyledons being sessile or petiolate is not stressed as an important character because it occurs in differently related groups. Also the arrangements of leaves as opposite or alternate is not a satisfactory basis for groupings because both arrangements can occur within the members of the same group, as in Groups I, II and III. The existence of 1 pinnate leaf or two opposite or even 3 pinnate leaves (in some Australian Acacias) is a matter of degree and not of quality.

The change from pinnate to bipinnate leaves is confirmed in the Sudan species and the phyllodic stage in the Australian species is a definite later development. The stipules change from foliate in Group III to scale-like in Group II and finally to spinescent. This is indicative of the direction of stipule evolution in the genus (fig. 1 page 36) and is correlated with similar trends in other organs. The cotyledons' shape agree with their seed shape, which is in turn characteristic of certain groups like the orbicular cotyledons of Group II, the oblong cotyledons of Group I and the obovate cotyledons of <u>A. albida</u> and the capitate climbers of Group III. The synopsis of the 4 seedlings groups produced here gives a more natural grouping of the Acacias because it is based on many attributes showing a correlation. The recent work by Robbertse and Schijff produced a grouping based on one character only, namely the petiolate or sessile cotyledons, which will definitely give an unnatural classification for an enormous genus like the Acacia.

C. ANATOMY

General

Previous anatomical studies on the Sudan and African Acacias were brief and not comprehensive. They were carried out as parts of the general studies of the anatomical characters of the family *Mimosaceae* or Order *Leguminosae* as a whole. A few specific anatomical studies were made on the Australian Acacias to investigate the nature of the phyllodes (Peters 1926). Timber anatomy was utilised by Chevalier (1928) to separate *A. albida* from the Acacias, and this led to wrong conclusions because *A. albida* was compared only with *A. nilotica*. D. F. Cutler (1969) also wrote a paper on the vegetative anatomy of the anamolous *A. albida*.

The present study presents comprehensive anatomical investigations on the Sudan Acacias for the first time. The study includes investigations on the primary root and shoot of the Acacia seedlings; it deals with the nodal anatomy of young and old stems in order to study the anatomical differences between spines and prickles; finally the timber anatomy of the Sudan species is described for the first time to assess its characters and their bearing on the general classification of the genus.

Materials and methods

Acacia seedlings were raised, as mentioned before (page 59), in glass-houses and left for 1-3 weeks to develop good roots and shoots. Then thin sections (10-20 μ) were cut using the slide microtome or hand sections at different levels along the seedling root, hypocotyl and stems. The sections were cut at different levels of the seedlings parts and transferred into a dish of sodium hypochlorite solution (e.g. undiluted Parazone for 5-30 minutes).

Sections were then transferred to a dish of water. Several changes of water were necessary to remove all traces of the Parazone solution. They were then transferred to 50% alcohol for 5 minutes and finally placed in the staining solution. Staining was done in one of two stain mixtures:

(a) Overnight staining:

Safranin 1% in 50% alcohol	95 parts
Delafields haematoxylin	5 parts

(b) Rapid staining:

Safranin 1% in 50% alcohol	90 parts
Delafields haematoxylin	10 parts

Staining time 2-4 hours

Both staining methods were used in this study. The sections were removed from the stain and put into 50% alcohol; after one minute they were removed and put in acid-alcohol (50% alcohol and few drops of HCl). Finally the sections were transferred rapidly to 50%, 70%, 90%, and absolute alcohol. Sections were then mounted directly on Euporal, or Canada Balsam, after transfer from absolute alcohol to xylene.

Sections for the nodal anatomy investigations were cut from young seedlings 1-3 weeks old and others from seedlings more than three weeks, and treated in the same manner as above. The timber anatomy sections were cut from mature timber blocks brought by the writer from the Sudan and selected from trees of 15 cm diameter, making sure that there was enough heartwood in the blocks. They were dipped in warm water for a week (in the case of hard timbers like that of A. nilotica they were dipped in 10% solution of hydrofluoric acid). Sections were then cut on a slide microtome, put for one hour in Parazone to clear, and then stained and mounted in the same manner as before. In addition to transverse sections of Acacia timbers, longitudinal sections were also made to study the structure of the timber rays.

1. Anatomy of the Acacia seedlings

The only previous work in this field which I know of was by Compton (1912) in his study of the seedling structure of the *Leguminosae* as a whole, and he investigated only some Australian Acacias.

The seedling roots: Sections were made at 1 mm below the proximal part of the seedling's root and downward to the distal part or the root cap.

The outline of the seedling root, in transverse section, was found to be terete in all the Acacias of Group I and II; *A. albida* has an undulating or grooved outline; the climbers of Group III have an angular, 4-sided outline.

Epidermis: Consists of 1-layered cells of different sizes, some are small and square-shaped and others rectangular; the outer wall of the epidermal cells is convex with a thin layer of cuticle.

Cortex: Consists of two parts - an outer layer consisting of small collenchyma, 1-3 cells thick, and an inner layer, 5-7 cells of parenchyma, getting wider and rounder as we go inwards.

Endodermis and pericycle: The endodermis consists of a layer of oval or elliptical cells bordering the cortex to the outside and the pericycle to the inside. The walls of the endodermis are thickened with Casparian strips; the cell contents are protoplasmic with many cell intrusions. The pericycle consists of a one layer of cells sheathing the vascular tissues to the inside.

Phloem: Consists of four groups of clear parenchyma cells surrounded by dense protoplasmic cells on the outside of the phloem groups.

Xylem: A tetrarch xylem star alternates with the four phloem groups. The large protoxylem vessels are to the inside and the small metaxylem vessels to the outside. At the apex of the root the pith is small and then englarges gradually towards the proximal end of the roots. At 1 mm below the proximal part of the root, the parenchymatous pith starts to force the xylem elements into a tangential position, forming a closed ring of wedge-shaped bundles with phloem elements still alternating with the xylem bundles. Thus the typical structure of the primary roots is established just before the root-stem transitional level.

The hypocotyl: At the proximal base of the hypocotyl the transition from root tissues to stem tissues has already started. At this transitional level, the protoxylem started to divide into two halves; thus there are produced four tangential bands of metaxylem with protoxylem on their eight margins. The phloem remains unchanged in position but is differentiated into sieve cells and companion cells with a sclerenchyma developing to the outside of the phloem. Cambium cells start to develop and spread from a position inwards against the phloem tissue to a tangential position opposite the xylem vessels and to the outside.

As we ascend the hypocotyl, the protoxylem which was divided into two halves, moves towards the inner and opposite part of the phloem and arranges itself in collateral bundles, with the protoxylem elements to the outside towards the phloem and the metaxylem elements to the inside towards the pith. The xylem elements are separated from the phloem by the vascular cambium which has now formed a continuous tangential layer of 2-4 cells around the xylem elements. Thus the typical structure of an endarch xylem with four vascular bundles is formed (see Plate 5 page 81).

At 1 mm below the cotyledonary node a pair of collateral bundles is produced leading to the cotyledonary petiole, and a median vascular tissue remains in the central stele which will continue along the stem. The four central and collateral bundles of the hypocotyl are continuously dividing, forming a continuous tangential ring of xylem elements towards the pith. The sclerenchyma sheath also divides to form a continuous sclerenchyma sheath around the phloem and cambium elements of the young stem.

This is the typical trend in the structural developments of the tissues of the root, hypocotyl and stem in the Sudan Acacias studied with one exception, i.e. A. albida. In this species, the transition from root to stem tissues does not start until 1 mm below the cotyledonary level, while in all other Acacias this transition starts at the junction between the root and the hypocotyl, or at most about 2 mm above the hypocotyl base (see Pls. 4-6 pages 80-82). This delay in transition from root to stem tissues is common in the Papilionaceae, less common in Caesalpiniaceae, but the Mimosaceae usually have low transitions (at hypocotyl base), Compton (1912). In the five Australian Acacias studied by Compton (1912), the transition was at a low level as in the Sudan Acacias studied here. This can be significant taxonomically as regards the position of A. albida amongst the Acacia group. Compton stated that the diameter of the axis of the hypocotyl is the most important factor in determining the level of transition; the bigger the diameter the lower the transition. This conclusion may be valid when comparing the three families in the Leguminosae and according to his conclusions

Plate 4. Anatomy of Acacia seedlings. Explanation in text.

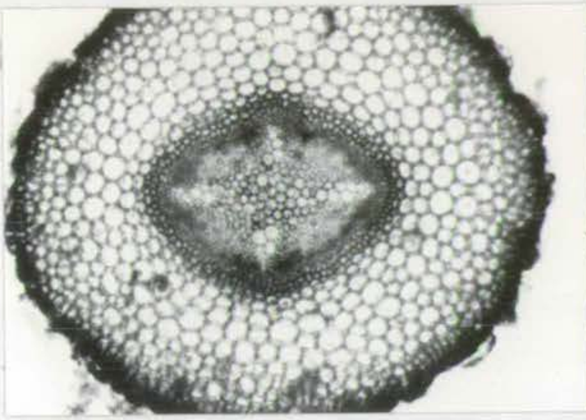
a. A. nilotica subsp. nilotica (x 80) T.S. of root tip.

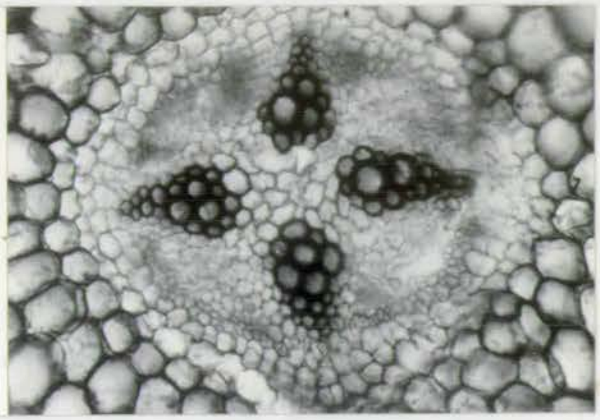
b. A. laeta (x 80) T.S. of root tip.

c. A. nilotica subsp. nilotica (x 64) T.S. 2 mm below root base.

d. A. laeta (x 80) T.S. 2 mm below root base.

e. A. senegal (x 56) T.S. 2 mm below root base.





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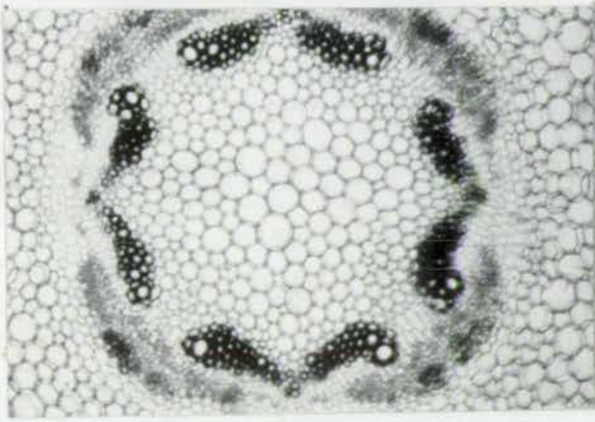

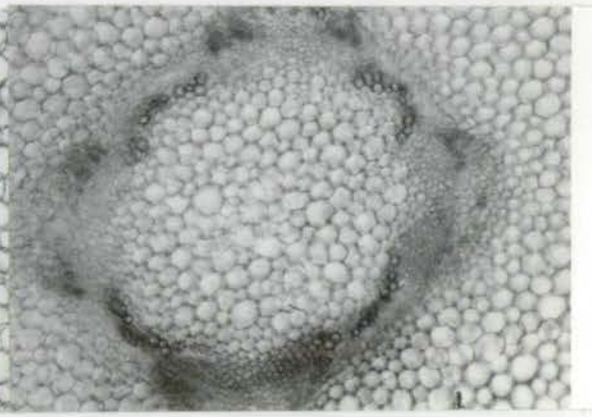

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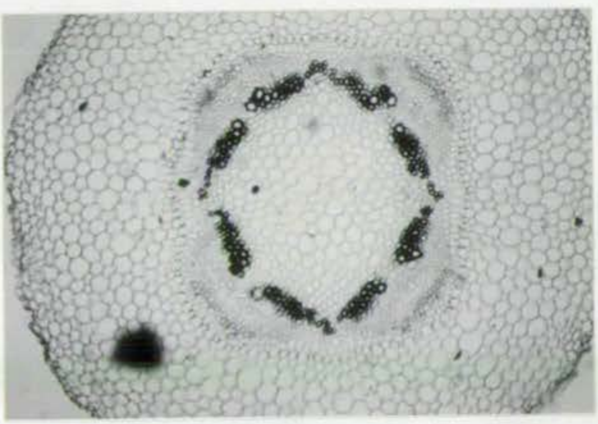

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Pl. 4

Plate 5. Anatomy of Acacia seedlings.

a. _A. nilotica_ subsp. _nilotica_ (x 64) T.S. 1 mm above hypocotyl base.

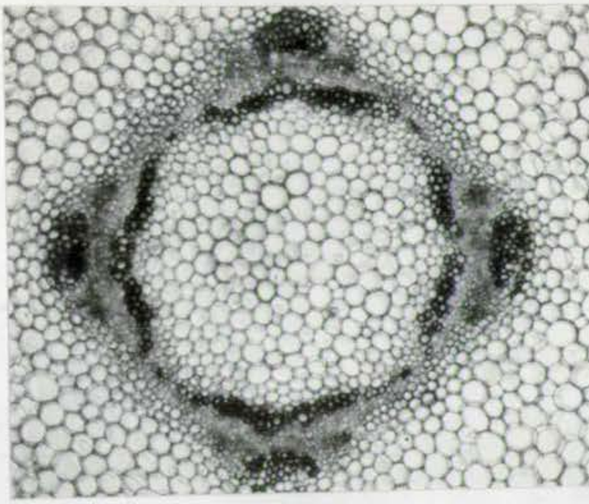
b. _A. nilotica_ subsp. _nilotica_ (x 56) T.S. mid hypocotyl.

c. _A. laeta_ (x 64) T.S. 1 mm above hypocotyl base.

d. _A. laeta_ (x 64) T.S. mid-hypocotyl.

e. _A. laeta_ (x 48) T.S. at cotyledonary level showing two pairs of vascular traces to the cotyledons and the central cylinder.

f. _A. laeta_ (x 48) T.S. below first node showing the central cylinder and three leaf traces on each side of the central cylinder indicating the first two opposite leaves.



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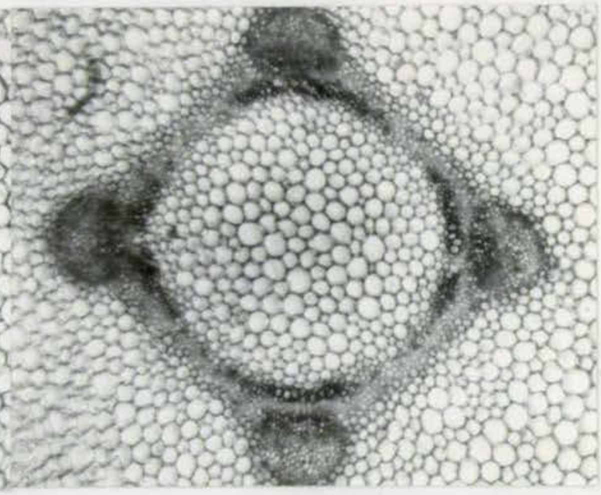

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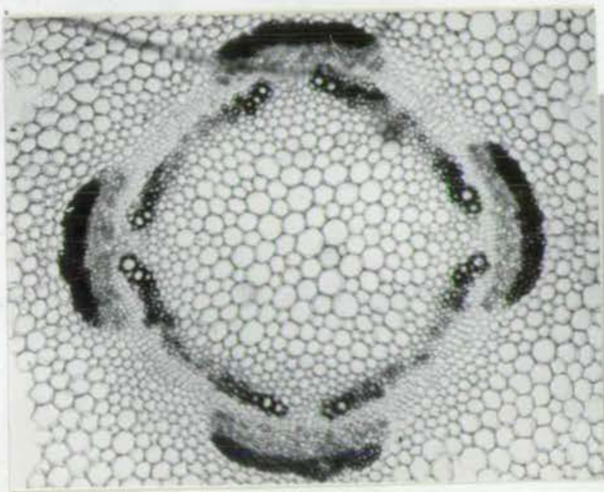

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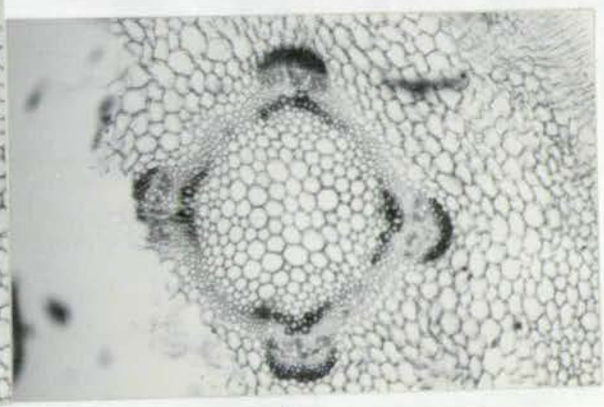

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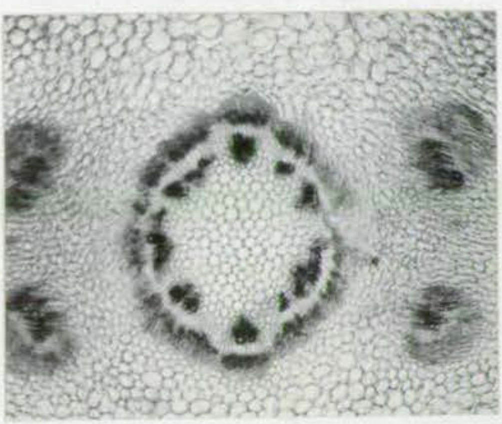

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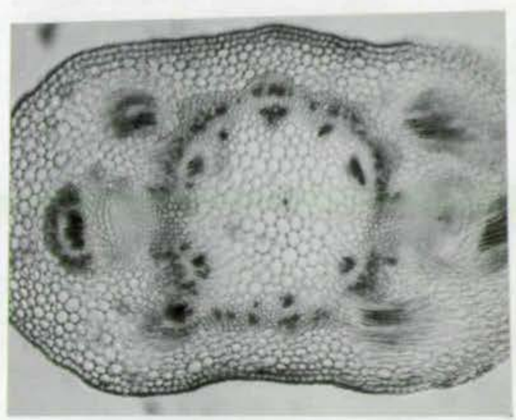

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Pl. 5

Plate 6. *A. albida* seedlings anatomy. Explanation in text.

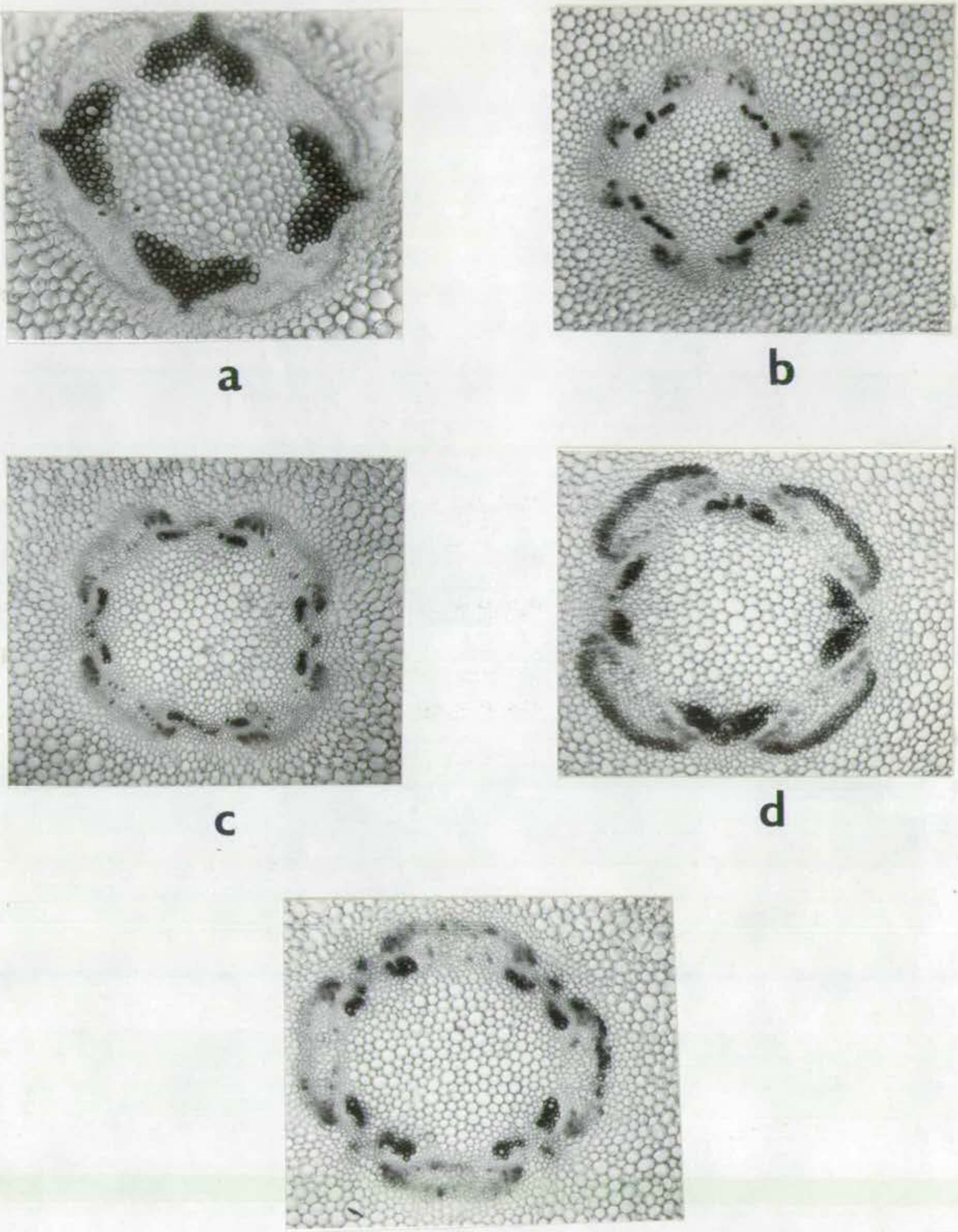
a. (x 64). T.S. below root base.

b. (x 56). T.S. 1 mm above hypocotyl.

c. (x 40). T.S. mid hypocotyl.

d. (x 64). T.S. mid hypocotyl.

e. (x 40). T.S. 1 mm below cotyledons.



a b c d e

Pl. 6

the Acacias have slender seedlings, and thus Compton put them in the small diameter category which should have consequently lower transition. In this study A. sieberana has a larger hypocotyl diameter than A. albida but the former conformed well with other Acacias in having low transition while A. albida did not.

2. Nodal Anatomy with special reference to spinescent and non-spinescent stipules

Previous work: The previous studies on the nodal anatomy dealt with the overall study of the Angiosperms, or with the whole characters of the Leguminosae and less specifically with the family Mimosaceae. A few Acacias were studied as a part of the Mimosaceae. Colomb (1887) studied Australian Acacias and was first to state the important fact that the vascular supply to a stipule is always a branch from that of the associated leaf. Sinnott (1914) maintained the taxonomic and phylogenetic importance of the number of gaps in regard to Angiosperm leaves and the nodal forms were divided into three types: "unilacunar", "trilacunar" and "multilacunar". He stated that the leaf of leguminous plants is almost always supplied with three foliar traces, each coming out of a separate gap in the vascular cylinder; this is the trilacunar type. Sinnott and Bailey (1914) showed that unilacunar nodes in the Angiosperms are mostly ex-stipulate, trilacunar ones mostly stipulate, while most multilacunar ones have sheathing leaf bases. S. Watari (1933) studied the vascular system in petioles and rachises of leguminous leaves; his study included three Acacia species of which one is African (A. nilotica). He concluded that the Mimosaceae have the trilacunar type of node and that the stipular traces are always supplied from the lateral foliar trace situated far from the medium one. Dormer (1945) investigated the taxonomic value of shoot structure in Angiosperms with special reference to the Leguminosae; he stated that the presence of free stipules with trilacunar nodes is a primitive character, as compared with stipules absent or adnate to the petiole with unilacunar or multilacunar nodes.

The present study on the nodal anatomy aims to investigate the nature of the vascular system of Acacia nodes and the difference, if any, of the prickles and spines. Sections were made 1 mm below and up to 1 mm above the nodes of the Acacia seedlings. The sections were treated as before.

Vascular systems to leaves and stipules: The circular stem in transverse sections of the Acacias changes to an oval shape a few mm below the next node, this sequence being repeated up the stem. The broader side of the oval stem starts to develop three lobes, the central lobe leading to the petiole and the lateral ones to the pair of stipules; the narrow side of the ovate stem has no lobes and is the opposite side of the leaf axil. The same trend takes place in the following node, except that the two sides are reversed because of the alternate leaf arrangement of the Acacias.

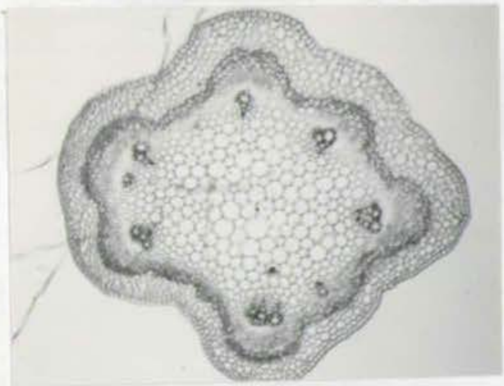
The tetrarch xylem divides, giving eight bundles which are arranged ovately in the central cylinder, bordered on the outside by a continuous layer of sclerenchyma sheath which encloses the phloem and cambium tissues respectively. Three leaf traces facing the leaf side leave the central vascular system and grow out laterally: the median trace goes towards the petiole lobe, and the lateral ones towards the stipular lobes. These lateral traces do not emerge from the median xylem elements, but from lateral traces situated far from the median one and separated by two xylem

Plate 7. Nodal anatomy. Explanation in text. A. polyacantha subsp. campylacantha.

a. (x 36) T.S. of stem before node.

b, c, d, e and f. (x 40) T.S. at node showing gradual stages of the development of the three leaf traces.

g. (x 40) T.S. at node showing stipular traces supplying the stipules and again joining the petiolar trace.



a

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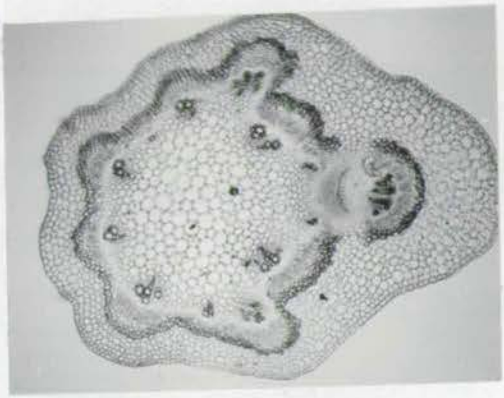

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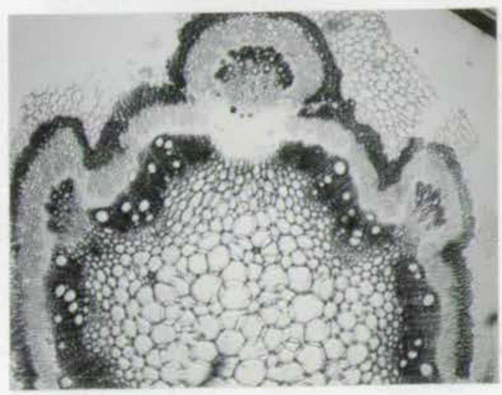

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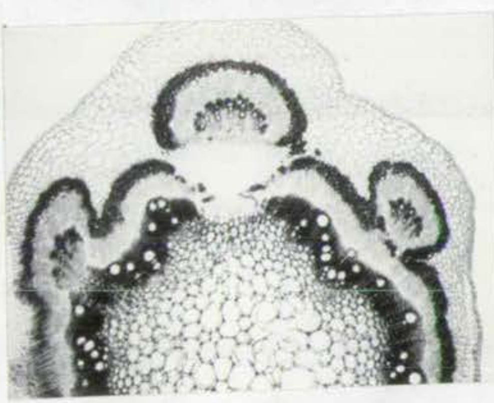

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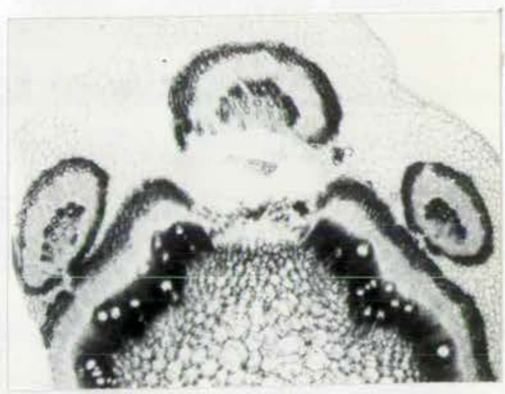

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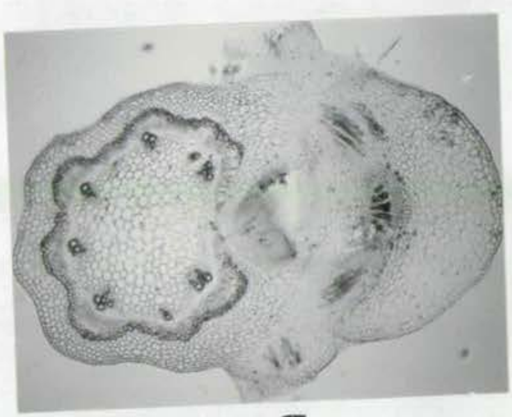


g

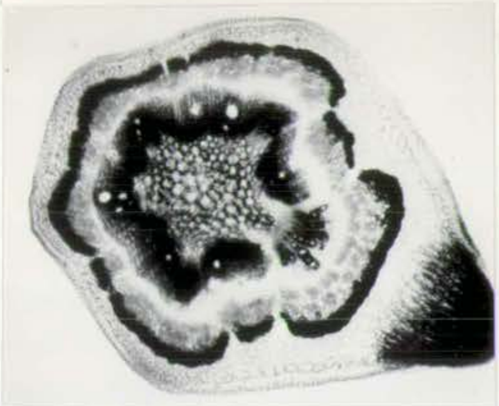
Pl.7

Plate 8. Nodal anatomy.

a, b and c. <u>A. senegal</u> (x 40) T.S. at node showing development of the three leaf traces.

d. <u>A. albida</u> (x 40) T.S. at node showing separation of leaf traces from central cylinder.

e. <u>A. mellifera</u> (x 80) T.S. at node showing vascular traces supplying one stipule (on the left) and the petiole (on the right).



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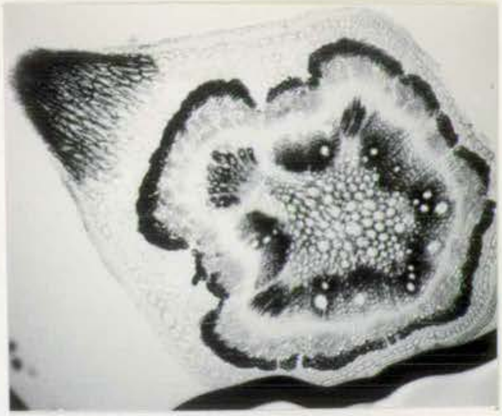

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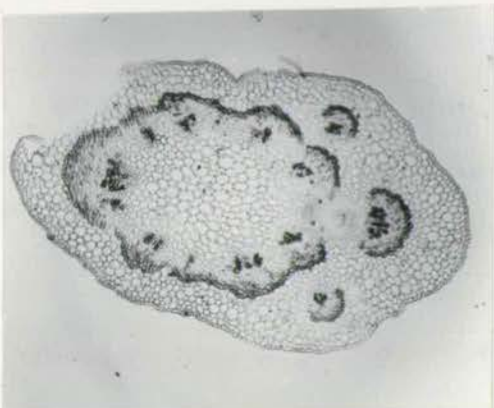

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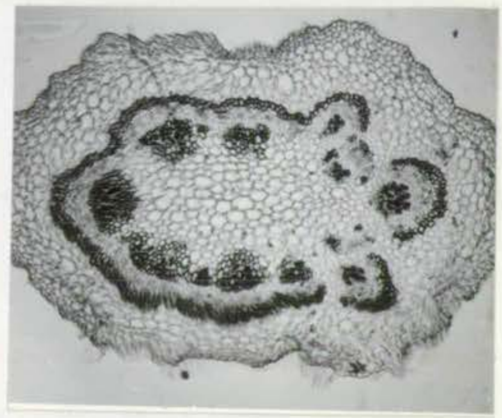


d

e

Pl. 8

elements which persist permanently in the central cylinder and start to divide to close the ruptured circle (Pl.7·e,f, page 85). The petule and the stipular traces carry with them an arc of sclerenchyma tissue which was lying opposite these traces before leaving the central cylinder; the sclerenchyma arcs soon encircle the three traces and form a ring on each of them. The ruptured central cylinder closes its circle again by division of the sclerenchyma and xylem elements to fill in the broken gaps. (Plates 7 & 8 pages 85 & 86).

This process of differentiation is repeated in all Acacias whether they have spinescent or non-spinescent stipules, thus showing a trilacunar node which is typical of the Mimosaceae. As the section comes up opposite the petiole level, the three ring traces change shape from the transverse position to longitudinal, the central one leading to the petiole and the lateral ones to the stipules, but joining again the petiolar trace (Plate 7 g, page 85). At this stage a circular group of cells may appear just below the petiolar trace, consisting of meristematic tissue which is an axial leaf bud. Above the nodal level the vascular cylinder of the stem attains its circular shape enclosed by the circular sclerenchyma sheath, and the transverse section of the stem again becomes circular at the internodes.

Spines and prickles: Members of Group I and IV are armed with spines, and those of Group II and III with falcate prickles. Anatomically, the spines being modified stipules have a vascular system and consequently are of endogenous origin. The prickles, on the other hand, whether they are on the nodes, internodes, rachis and rachillae, arise as outgrowths of the epidermis which elongates and the cortical part is occupied by parenchyma tissue which is an extension of the stem cortex; these tissues harden to

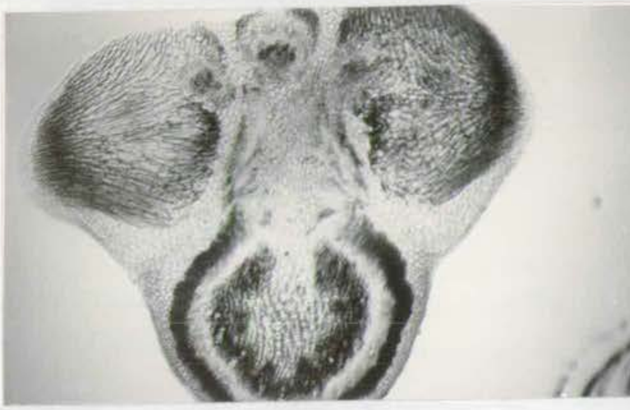
Plate 9. Anatomy of the spines.

a and b. A. albida (x 48) T.S. at node showing in a. the development of the spines, and in b. the vascular system supplying the two spines.

c. A. tortilis subsp. spirocarpa (x 40) T.S. at node showing a pair of spines with a vascular supply.

d. A. seyal var. seyal (x 48) T.S. at node showing one spine with a continuous vascular supply.

e. A. nilotica subsp. nilotica (x 40) T.S. at node showing a pair of spines with a vascular supply.



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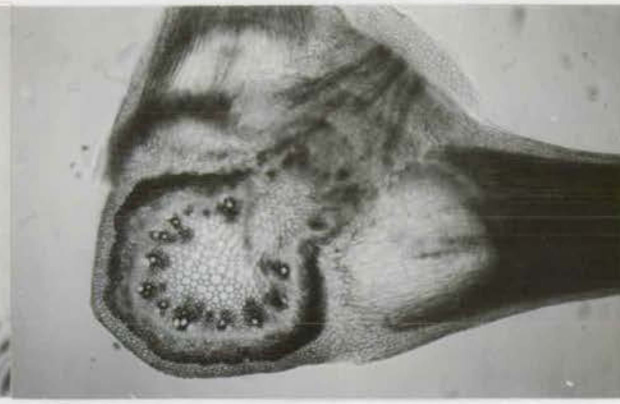

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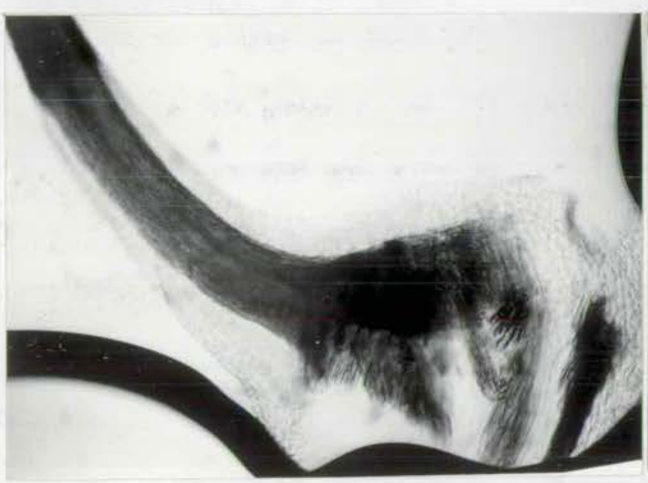

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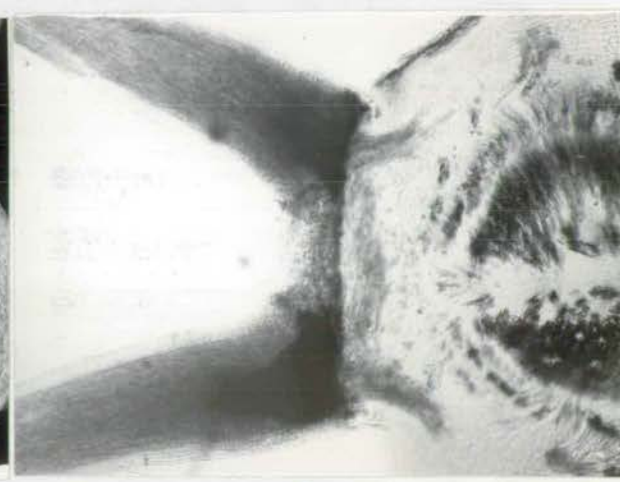

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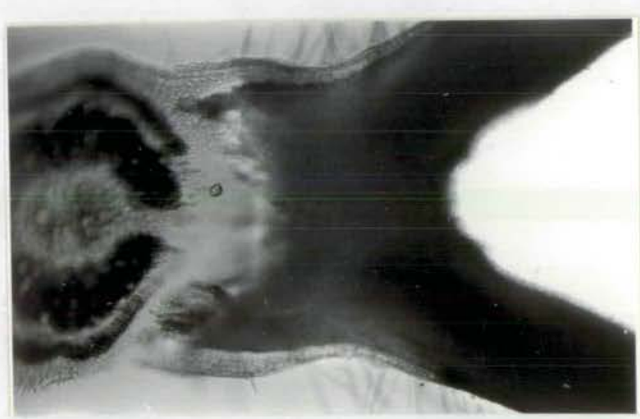


e

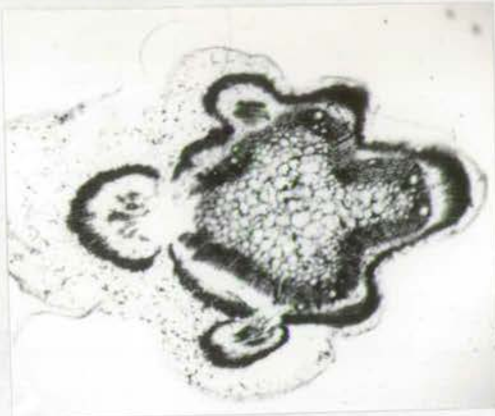
Pl. 9

Plate 10. Anatomy of the prickles. Explanation in text.

a, b and c. A. ataxacantha (x 40) T.S. at node in a. showing development of leaf traces to the petiole and stipules; no prickles are apparent; b. T.S. at stem showing exogenous development of prickles; c. T.S. on stem showing final development of prickles without vascular supply.

d. A. polyacantha subsp. campylacantha (x40) T.S. at node showing one prickle without vascular supply.

e. A. laeta (x 40) L.T.S. at node showing one prickle with no vascular supply.



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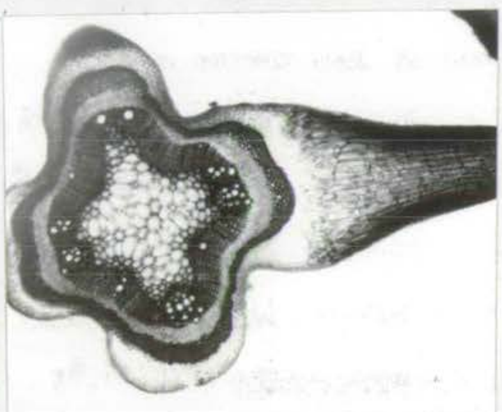

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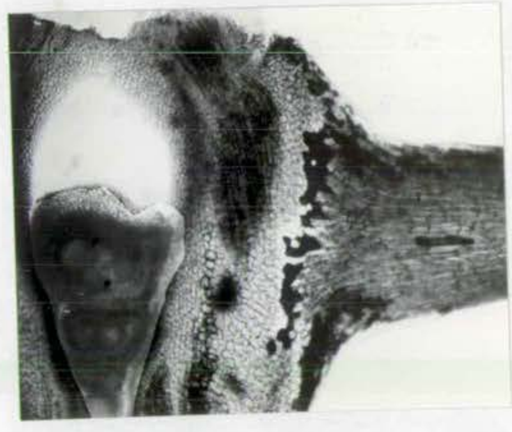


e

Pl.10

form the prickles which are devoid of vascular tissue and are thus of exogenous origin (see Plates 9 & 10 pages 88 & 89).

The hooked prickles of A. tortilis and A. reficiens, together with those of A. macrothyrsa conform anatomically with the type of their Group I, irrespective of their prickle shapes. Similarly A. dolichocephala and A. horrida also agree anatomically with the type of Group I to which they belong irrespective of their inflorescence types.

The epidermal, non-vascular prickles are consistent also in all the members of Group II and III without any exception.

3. Timber Anatomy

Introduction: Although some Acacia timbers have been described before, there was no taxonomic treatment of the timber anatomy of the Acacias. Bailon (1863) and Chevalier (1934) both dealt with the timber anatomy of A. albida as compared with A. nilotica, but because they were not dealing with a large number of species, they assumed that the uniseriate rays of A. albida are exceptional in the genus, a conclusion which will be proved in this work to be untrue. La bacq (1957) worked also on the timber anatomy of A. albida, but as mentioned by Cutler (1969) La bacq must have been working on an incorrectly identified specimen which had multiseriate rays, a character not present in A. albida timber.

The timber anatomy of some of the Acacias was described by Pearson and Brown (1932) in studying the commercial timbers of India; among the species studied in their work is A. nilotica which is also an African species. Their study was from a commercial forestry viewpoint and not taxonomic. Metcalfe and Chalk (1952) discussed generally the anatomical characters of the order

Leguminosae. Cutler (1969) made a special study of the vegetative anatomy of A. albida and emphasized the lack of literature on the subject; he gave detailed descriptions of the anatomy of the petiole, leaf, twig, matured wood and theroot of A. albida.

The present work deals with the timber anatomy of the Sudan Acacias, aiming towards employing the timber characters taxonomically, in showing affinities and relationships amongst the studied species.

The method of preparing the timber sections for study was already described on page .

Terminology: The following terminology explains the method of description of timber characters in this text with explanatory diagrams.

Vessels:

Number of pores: Number of vessels per square cm seen in transverse section arranged solitary or in aggregate groups.

Diameter: Diameter of vessels in μ (= Dμ).

Rays:

Parenchyma rays seen in longitudinal sections.

Type of ray: Whether it is uniseriate, biseriate or multiseriate referring to the number of cells along the width of rays.

Homogeneous rays: Rays having uniform cells.

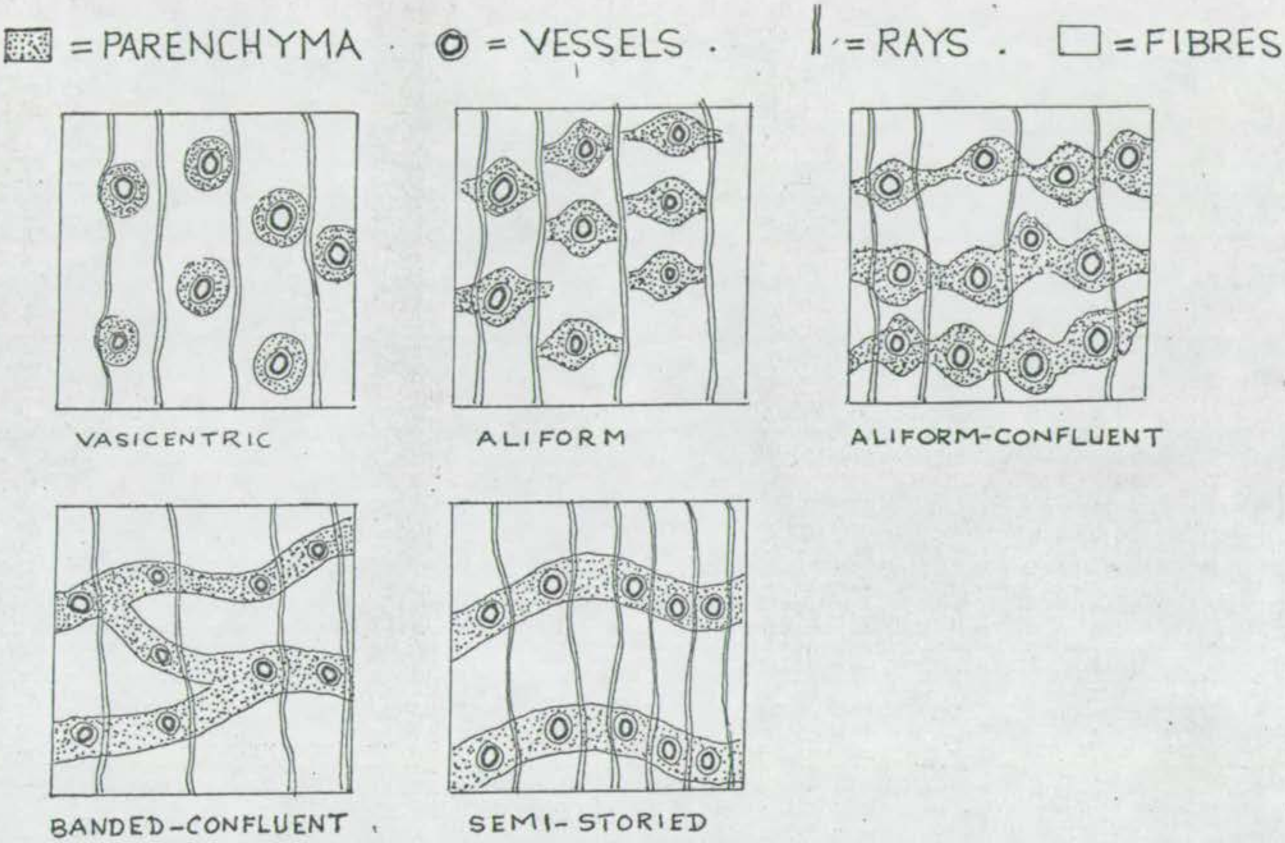
Heterogeneous " : " " cells of different shapes and sizes.

Number of rays : Number of rays per square cm (= No./sq.cm).

Width of ray : Related to seriation and is the number of cells along the width of the ray, ranging from 1-12 cells (W in cells).

TIMBER ANATOMY

PARENCHYMA TISSUE (T.S.) IN SUDAN ACACIAS:



RAY TYPES (L.S.) IN THE ACACIAS (HOMOGENEOUS RAYS):

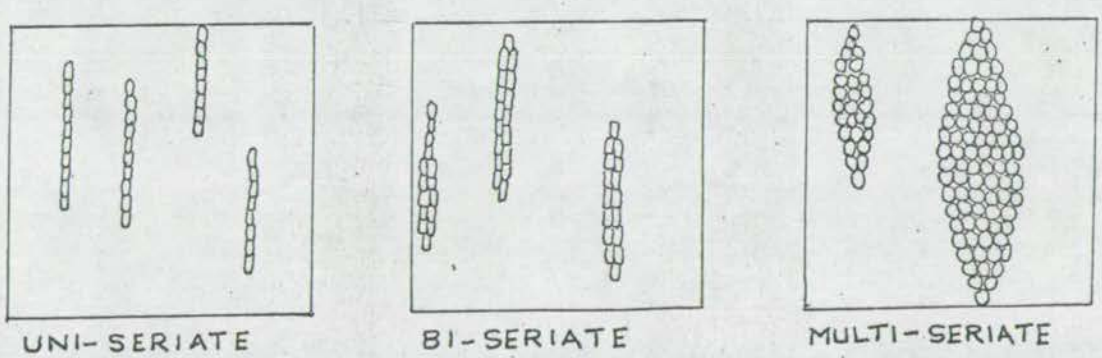


FIG.11 WOOD ANATOMY TERMINOLOGY

TABLE NO. 3 SHOWING TABULATED CHARACTERS OF THE TIMBER ANATOMY OF THE STUDIED ACACIAS

Name	Vessels (Pores)		Rays			Parenchyma	Fibres
	No/sq cm	D	No/sq cm	Type	W in cells	Type	Type
Group I							
1. A. ehrenbergiana	13	10	20	Multi	1-12	confluent	dominant
2. A. gerrardii	8	10	26	"	1-8	"	"
3. A. sieberana	10	10	35	"	1-8	"	" or equal
4. A. drepanolobium	14	10	20	"	1-7	"	" " "
5. A. nilotica	11	11	21	"	1-6	vasicentric & confluent	dominant
6. A. tortilis	10	8	20	"	1-8	confluent to aliform	"
7. A. seyal	16	11	27	"	1-10	confluent	"
8. " var.fistula	16	10	27	"	1-12	"	"
9. A. nubica	10	10	20	"	1-6	"	"
Group II							
10. A. laeta	18	8	35	"	1-4	aliform	"
11. A. asak	14	10	45	"	1-4	"	"
12. A. polyacantha	12	11	30	"	1-6	vasicentric	"
13. A. mellifera	15	10	27	"	1-4	confluent	"
14. A. senegal	14	10	41	"	1-4	aliform	"
Group III							
14. A. ataxacantha	20	6	63	Uni & bi	1 or 2	vasicentric	"
15. A. brevispica	90	4	60	"	1 or 2	"	"
16. A. schweinfurthii	90	3	90	"	1 or 2	"	"
Group IV							
17. A. albida	4-6	15	60	"	1 or 2	storied confluent	less or equal to parenchyma

<u>Parenchyma type</u>: (see figure)

Aliform, confluent, vasicentric.

<u>Fibres types</u>: (see figures)

Dominant: covering most of the wood matrix

Equal to parenchyma layer

Less than parenchyma layer

Abbreviations in bracket refers to the corresponding attribute in Table No. 3 p

<u>Characters of the Acacia wood anatomy</u>: The sap wood is white to yellow-white; heartwood dark brown, red, pink to almost black. The timber itself is hard and heavy. Growth rings are absent in the Acacia wood.

Vessels: Diffuse, solitary or multiples of 2-6 vessels. The frequency of the pores varies from 4-90 per square cm in transverse section. The diameter of the pore ranges from 3μ to 15μ. Tyloses are absent. The pits are circular or oval, bordered and are of the vestured type (cribriform membrane). Wall thickening is thicker in the northern arid species. The vessel pores are of different sizes and shapes ranging from circular, oval and semicircular. The vessels are always surrounded by parenchyma cells.

Parenchyma: All Acacias have the paratracheal type of parenchyma, i.e. parenchyma cells are surrounding the vessels. The paratracheal parenchyma is found as vasicentric, i.e. a layer of parenchyma cells sheathing the vessels, or confluent, i.e. wavy bands of parenchyma cells, or aliform, i.e. a vessel is surrounded by elongate-diamond-shaped parenchyma tissue, or a mixture of aliform and confluent types. In <u>A. albida</u> we get semi-storied confluent parenchyma. The cells in this are polygonal or round with variable thickening of the walls; the pits are simple and oval. The cells always contain rhombohedral or rectangular crystals. Other cell

Plate 11. Timber anatomy. Explanation in text.

a. _A. sieberana_ (x 100) T.S. of wood showing confluent parenchyma.

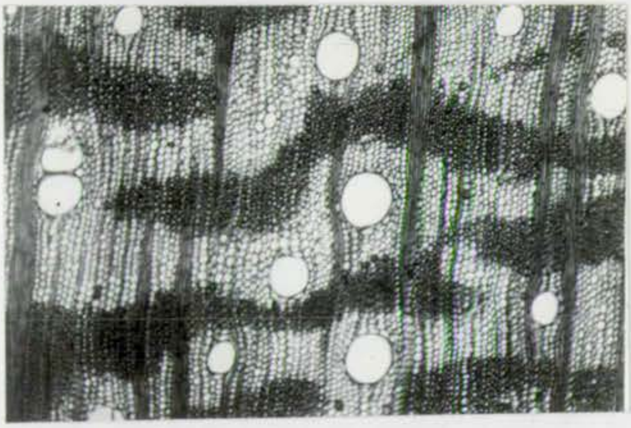
b. _A. sieberana_ (x 100) L.T.S. of wood showing multi-seriate rays.

c. _A. drepanolobium_ (x 56) T.S. of wood showing confluent parenchyma.

d. _A. drepanolobium_ (x 56) L.T.S. of wood showing multi-seriate rays.

e. _A. seyal_ var. _fistula_ (x 100) T.S. of wood showing confluent parenchyma.

f. _A. seyal_ var. _fistula_ (x 100) L.T.S. of wood showing multi-seriate rays.



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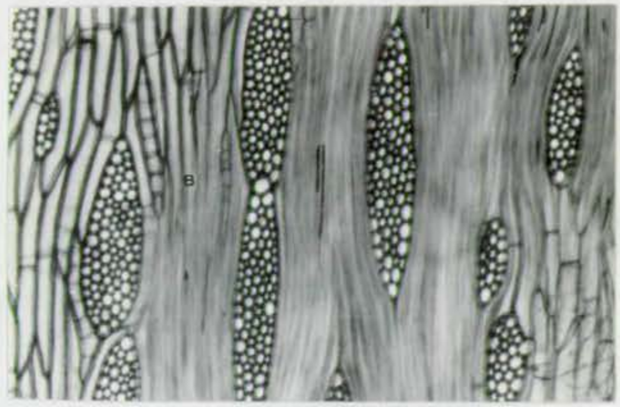

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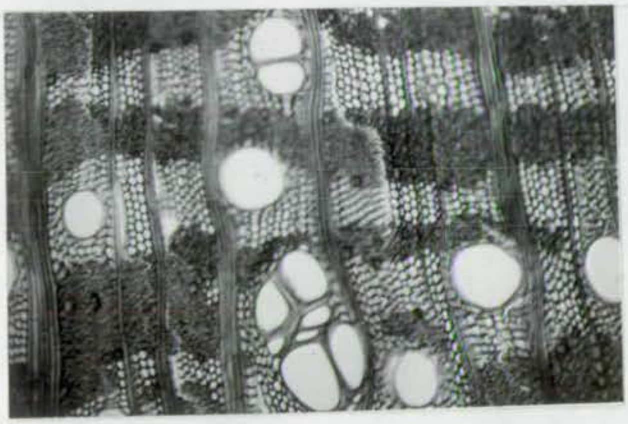

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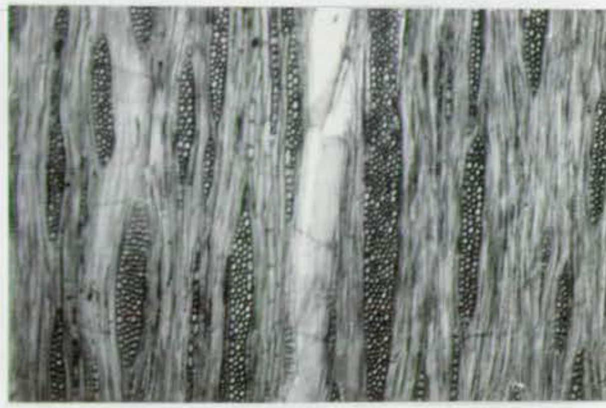

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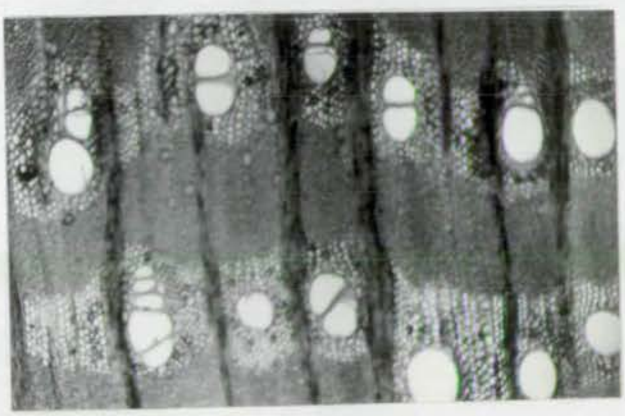

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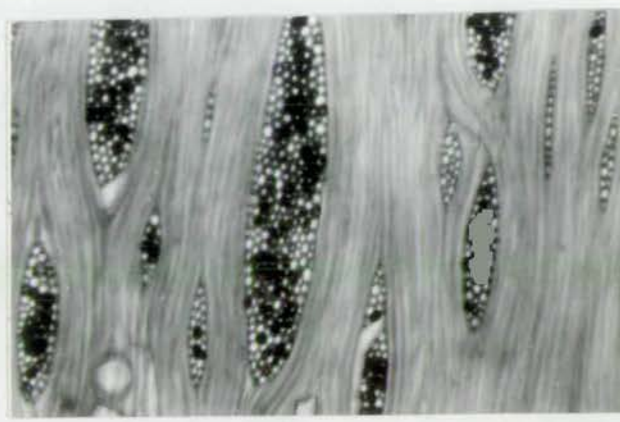

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Pl.11

Plate 12. Timber anatomy.

a. _A. tortilis_ subsp. _raddiana_ (x 42) T.S. on wood showing confluent parenchyma.

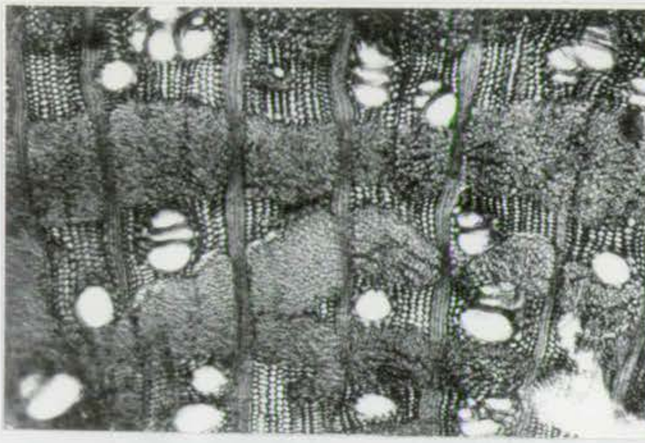
b. _A. tortilis_ subsp. _raddiana_ (x 42) L.T.S. on wood showing multi-seriate rays.

c. _A. seyal_ var. _seyal_ (x 40) T.S. on wood showing confluent parenchyma.

d. _A. seyal_ var. _seyal_ (x 56) L.T.S. on wood showing multi-seriate rays.

e. _A. gerrardii_ (x 100) T.S. on wood showing confluent parenchyma.

f. _A. gerrardii_ (x 100) L.T.S. on wood showing multi-seriate rays.



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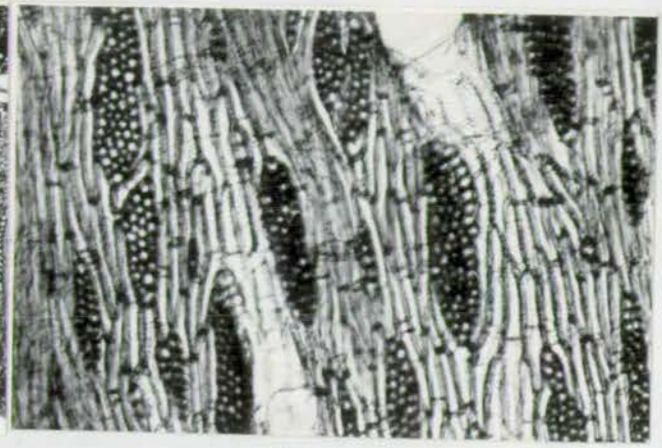

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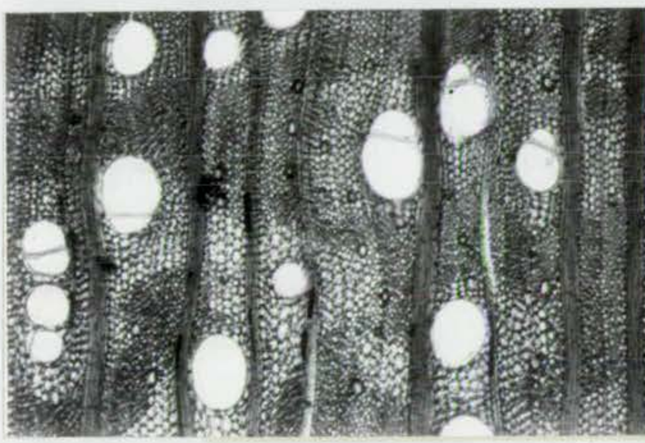

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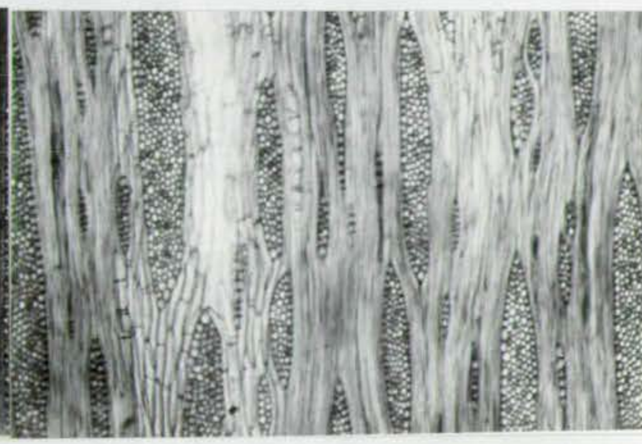

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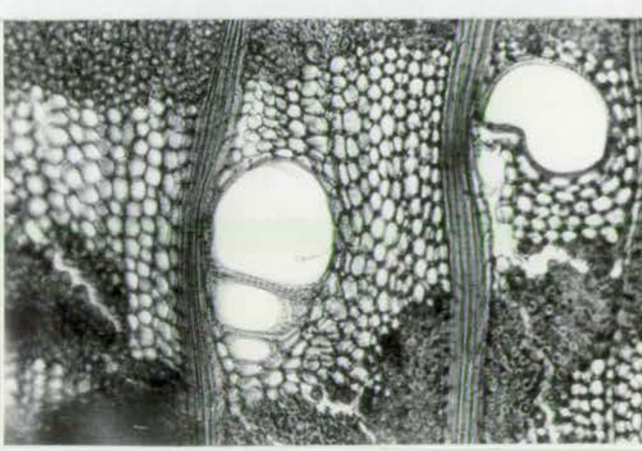

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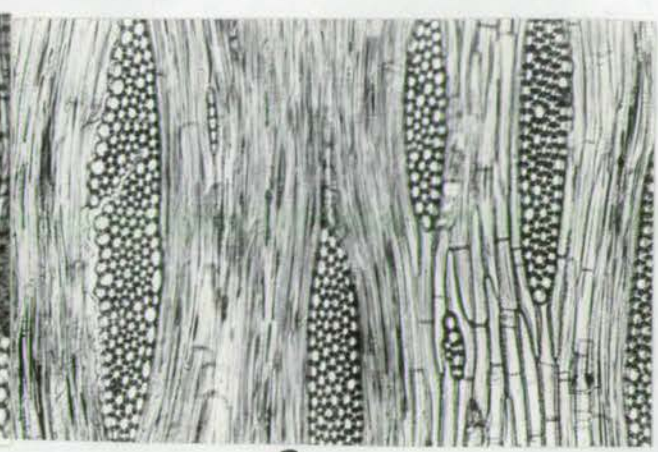

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Pl. 12

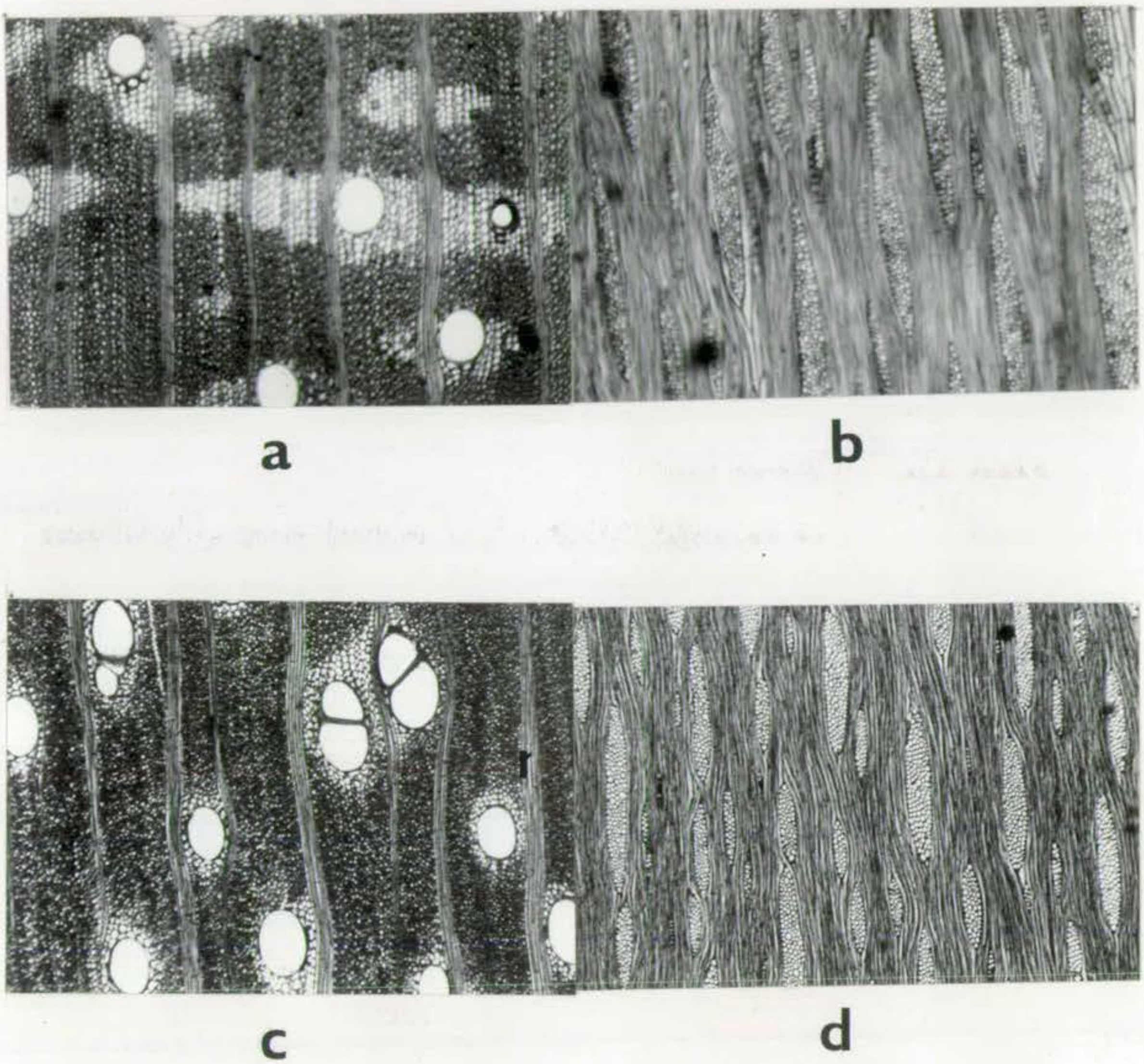
Plate 13. Timber anatomy.

a. <u>A. nubica</u> (x 56) T.S. on wood showing confluent parenchyma.

b. <u>A. nubica</u> (x 56) L.T.S. on wood showing multi-seriate rays.

c. <u>A. nilotica</u> subsp. <u>nilotica</u> (x 36) T.S. on wood showing confluent parenchyma.

d. <u>A. nilotica</u> subsp. <u>nilotica</u> (x 45) L.T.S. on wood showing multi-seriate rays.



Pl.13

Plate 14. Timber anatomy.

a. _A. senegal_ (x 45) T.S. on wood showing confluent parenchyma.

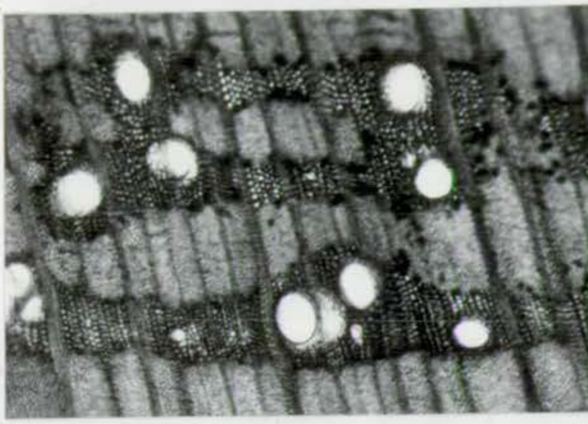
b. _A. senegal_ (x 80) L.T.S. on wood showing multiseriate rays.

c. _A. mellifera_ (x 36) T.S. on wood showing aliform-confluent parenchyma.

d. _A. mellifera_ (x 36) L.T.S. on wood showing multiseriate rays.

e. _A. laeta_ (x 36) T.S. on wood showing aliform parenchyma.

f. _A. laeta_ (x 36) L.T.S. on wood showing multiseriate rays, 3-4 cells wide.



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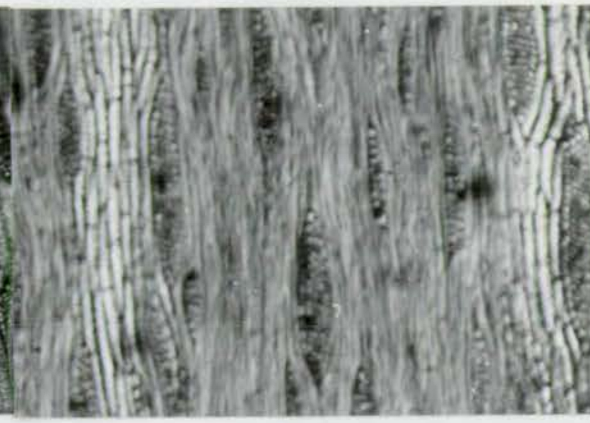

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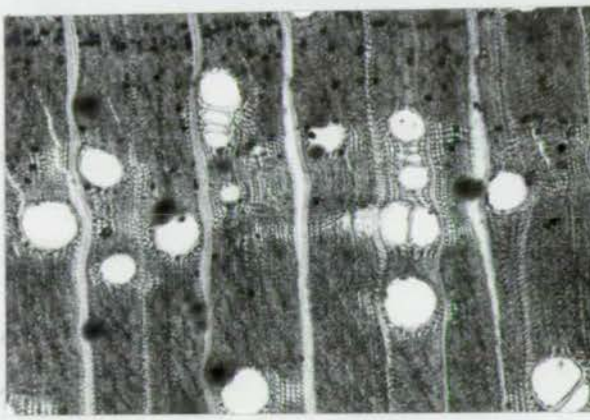

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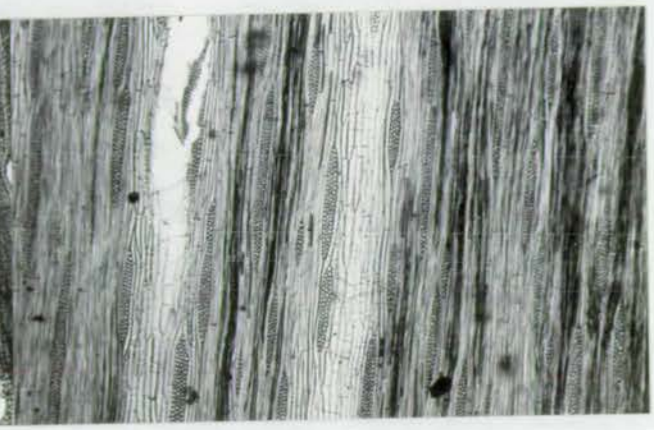

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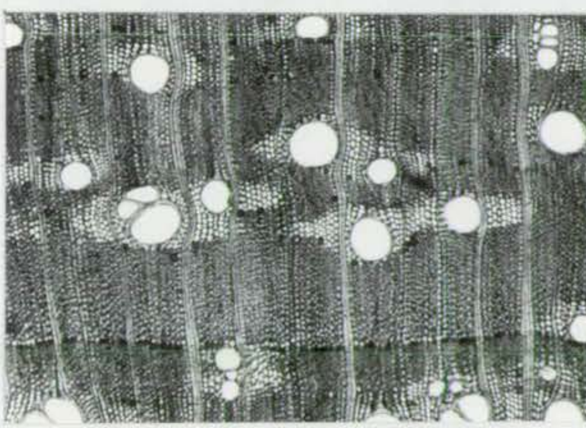

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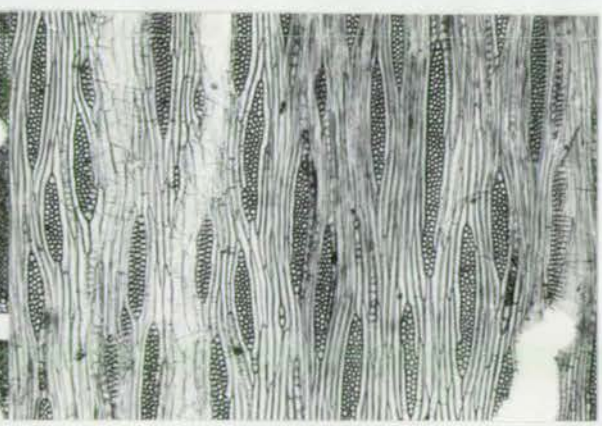


f

Pl.14

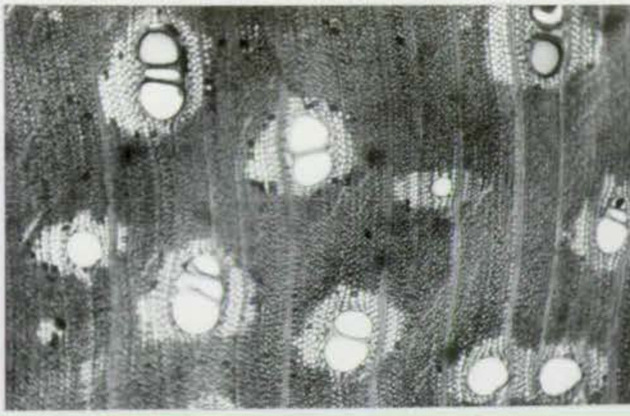
Plate 15. Timber anatomy.

a. *A. asak* (x 36) T.S. on wood showing aliform parenchyma.

b. *A. asak* (x 36) L.T.S. on wood showing multi-seriate rays, 3-4 cells wide.

c. *A. polyacantha* subsp. *campylacantha* (x 36) T.S. on wood showing vasicentric parenchyma.

d. *A. polyacantha* subsp. *campylacantha* (x 36) L.T.S. on wood showing multi-seriate rays, 3-6 cells wide.



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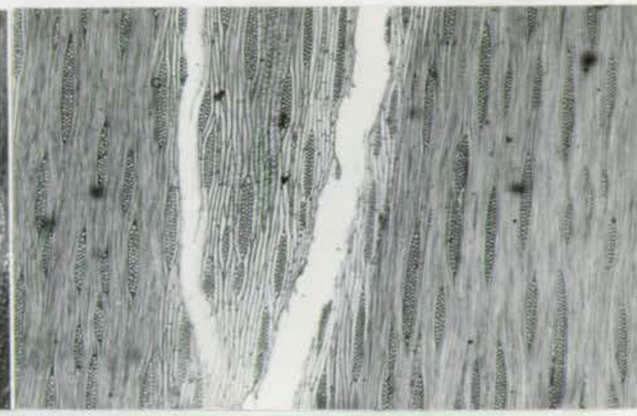

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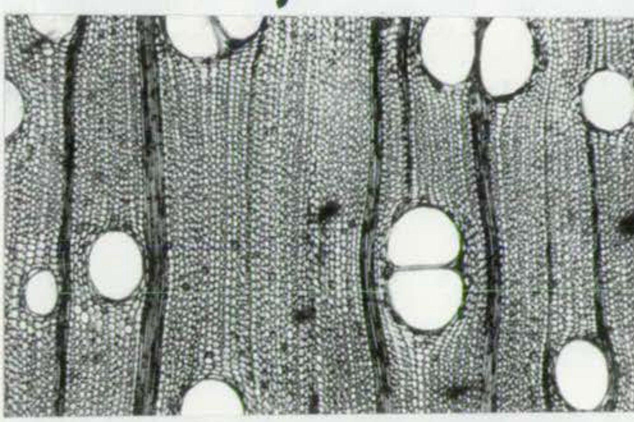

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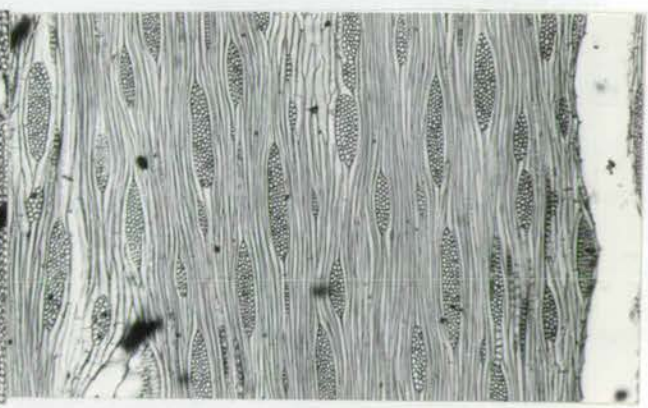


d

Pl.15

Plate 16. Timber anatomy.

a. A. ataxacantha (x 42) T.S. on wood showing vasicentric or absent parenchyma.

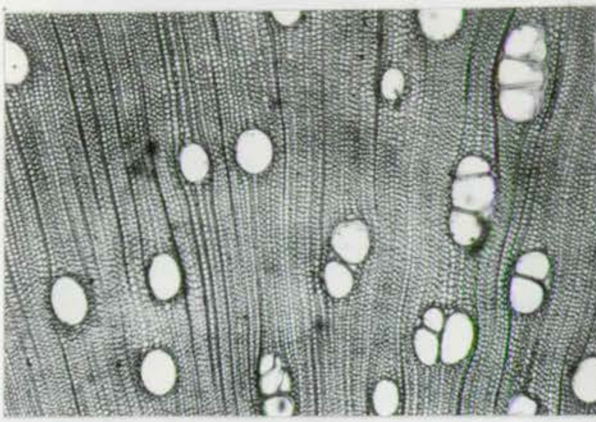
b. A. ataxacantha (x 42) L.T.S. on wood showing uni- and bi-seriate rays.

c. A. brevispica (x 130) T.S. on wood showing vasicentric or absent parenchyma.

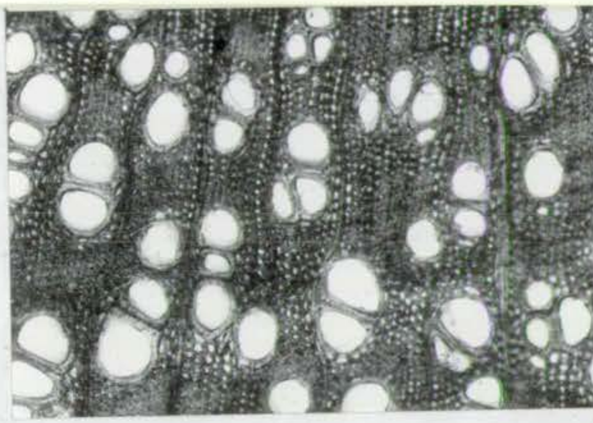
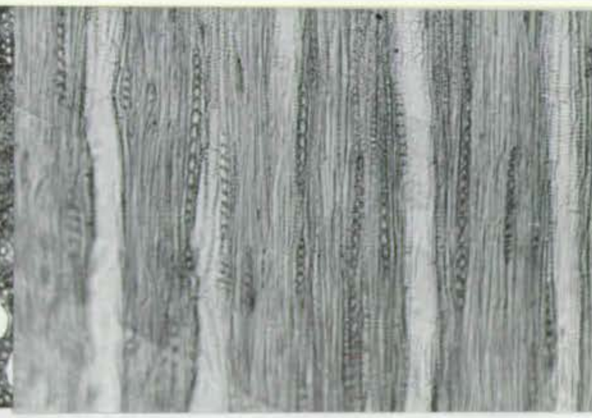
d. A. brevispica (x 130) L.T.S. on wood showing uni-seriate rays.

e. A. schweinfurthii (x 112) T.S. on wood showing vasicentric parenchyma.

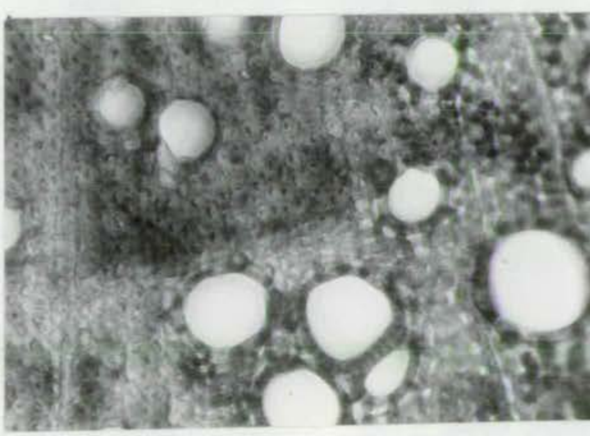
f. A. schweinfurthii (x 180) L.T.S. on wood showing uni-seriate rays.




a b

c d



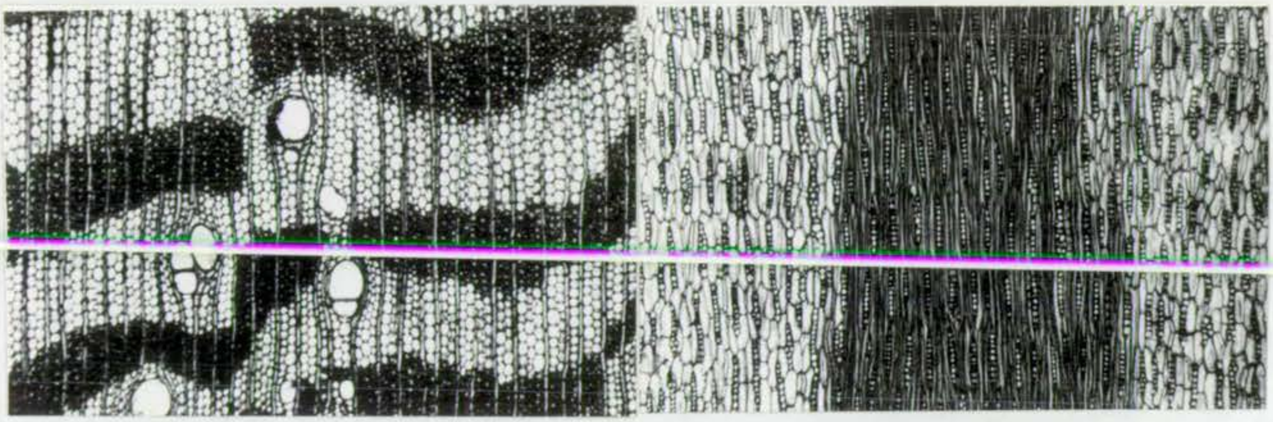

e f

Pl.16

Plate 17. Timber anatomy.

a. A. albida (x 36) T.S. on wood showing semi-storied parenchyma.

b. A. albida (x 36) L.T.S. on wood showing uni- and bi-seriate rays.



a b

Pl.17

intrusions are tannins, starch grains and gummy materials.

Fibres: The fibrous tissue usually constitute the dominant tissue in the wood matrix. The fibre cells are usually thick walled, gelatinous and non-septate. In few cases, as in A. albida, A. sieberana and A. drepanolobium, the fibrous tissue is almost equal to the parenchyma tissues.

Rays: Rays in the Acacias are of the homogeneous type, i.e. all ray cells are of the procumbent type. The rays types differ in the groups by being of the multiseriate or bi-and uniseriate types. This refers to the width of the ray being formed of many cells, two cells or one cell respectively. The number of rays per square mm ranges from [illegible] and varies with the different taxonomic groupings in the genus. It is well correlated with the width of the ray cells and their lengths as well. Dark amorphous materials of gums and tannins are present in the ray cells.

The above tissues, namely vessels, parenchyma, fibres and rays, are exemplified in Figs.11 page 92 to show their different patterns and the terms used in this description.

The data collected from the individual species which were studied are shown in Table No.3 page 93.

Summary and discussion of the timber characters

There are definite patterns which characterise certain groups and there is a good indication of certain trends in the evolution of the infra-generic groups. The results are not valuable at the species level as has been stated before by Metcalfe and Chalk (1952) in their study of the Leguminosae.

The following analysis shows the timber characters of the four Acacia groups suggested in this study (see Pls.11-17 page 95-101).

Group I: The parenchyma tissue in this group is of the confluent type, with one exception - A. nilotica, which is of the confluent type together with vasicentric type. In some cases, as in A. sieberana and A. drepanolobium, the parenchyma tissue almost equals the fibrous tissue in abundance. The species of this group usually grow in Central and Northern Sudan where conditions are arid. The number of pores per square cm varies from 8-16 and the pore diameter from 8-11 μ. The rays are long and multiseriate, 1-12 cells wide and mixed with the multiseriate are many uni and biseriate rays. The number of rays per square cm ranges from 20-35.

As is shown in Table 3 page 93, the members of this group have the highest amounts of parenchyma and lowest amounts of fibres as compared with the other groups, except A. albida. The group also has the longest and widest multiseriate rays amongst the Acacias.

Group II: The parenchyma in this group is variable. The vasicentric type occurs in one species, A. polyacantha, which grows in South Sudan in humid habitats. Then there is the aliform type represented in A. laeta, A. senegal and A. asak, and finally we get the confluent type (as in Group I) in A. mellifera, a species always growing with members of Group I in Northern Sudan. The fibrous tissue in this group is always more abundant than the parenchyma tissue. Pore number ranges from 12-18 and the pore diameter has a range of 8-11 μ. The rays in this group (like Group I) have the multiseriate type mixed with uni and biseriate types, but the length and width of the rays are very much reduced in size. The width of the multiseriate rays ranges from 1-4 cells wide, as compared with

1-12 in Group I. Consequently the number of rays per square cm has increased and ranges from 27 to 45.

<u>Group III (Climbers)</u>: Members of this group have homogeneous timber characters. Parenchyma is very much reduced and confined only to the vasicentric type. In some specimens the parenchyma almost completely disappears and the whole matrix is occupied by fibrous tissue or else some scanty parenchyma appears around the vessels, as in <u>A. ataxacantha</u> and <u>A. schweinfurthii</u>. The pores in this group increase in number and range from 20, as in <u>A. ataxacantha</u>, to 90, as in <u>A. brevispica</u> and <u>A. schweinfurthii</u>. The diameter of the pore is reduced to its smallest size and varies from 3-6 μ. The rays in this group are much specialised and have evolved into uniseriate rays with few biseriate rays, but with complete absence of the multiseriate rays of Groups I and II. The number of rays has increased tremendously and ranges from 63 to 90 rays per square cm.

<u>Group IV</u>: The timber characters of this monotypic group, containing only <u>A. albida</u>, are very different from all the other species of Acacias so far studied.

The parenchyma is aliform-confluent but is more abundant than the fibres, and is arranged in semi-storied bands. Embedded in the parenchyma are the vessels which are few, 4-6 per square cm, and have a large pore of 15 diameter. The rays are small but many, 60 per square cm, and are all uniseriate or occasionally biseriate. This last character is common with Group III. The difference as a whole is the presence of this storied type of parenchyma, fibres, vessels and rays. This storeying (echolon) is characteristic of the more advanced family <u>Papilionaceae</u>, but completely absent in the Mimosaceae as a whole.

Evolutionary conclusion

On the basis of the above data there seems to be certain trends in the change of certain tissues of the Acacia species studied. A trend in the parenchyma tissue to change gradually from confluent - aliform - vasicentric - absent. This change occurs from Group I, II to III. Another trend occurs in the pore characters where there is a change from few and large to many and smaller, and the last trend in the character of the rays from large and few to many and smaller, as well as a decrease in the width of the rays, i.e. from multiseriate to uniseriate. All these characters emphasize a trend from Group I to Group III, keeping A. albida out as an exceptional type of timber.

The phylogenetic direction of these trends is difficult to interpret at this stage, but taking the literature on the wood Anatomy, Metcalfe & Chalk (1952), Kribs D. (1935), Senn (1943), Jane (1956) and others, it seems that there is a universal agreement now that vasicentric parenchyma is advanced as compared to aliform and confluent parenchyma; and also that uniseriate rays are advanced compared to multiseriate rays. According to these assumptions, it seems that the Acacia's timber is evolving from the timber of Group I to II to III. A. albida, according to this assumption, has a mixture of advanced characters, like uniseriate rays, and primitive ones, like banding parenchyma tissue, which really emphasizes this species unique position.

There is also an agreement amongst workers in this field that uniseriate rays is an advanced character as compared to bi- and multiseriate rays. This would put Group III as the most advanced type of timber and Group I as the most primitive type with Group II as intermediate.

D. PALYNOLOGY

Earlier work

Acacia pollen was first figured by Kunth (1819) showing the polyad arrangement. Mohl (1834) made a detailed work on the pollen grains of many families including the Mimosaceae, and described the Acacia polyads. Rosanoff (1866) studied Acacia pollen and has shown that there took place in the pollen mother cell two successive divisions resulting in the formation of four cells separated by clearly defined walls, and that these arranged themselves in the same plane in a tetrahedral arrangement. Each of these daughter cells appear to divide twice more, producing four cells which assume the final tetrahedral arrangement.

Then Wodehouse described the 16-celled polyads of the Acacias and showed diagramatically the special arrangement of cells which produce the most compact arrangement. He employed pollen morphology with other morphological characters in suggesting the possibility of subdividing Mimosaceae.

Some fossil studies were done by Selling (1948) on Hawaiian species as well as by Cookson (1953) on Australian species; both showed the presence of 8-16 cells polyads.

In 1955 J. A. Coetzee worked on South African and some Australian species and arranged the Acacias firstly into the traditional inflorescence groups and then the pollen groups into fissured or non-fissured pollens. The spicate Acacias have non-fissured pollen and the capitate species fissured pollens.

As two species, A. pennata (A. brevispica pro parte) and A. detinens, do not fit into these inflorescence-pollen groups, she put them into a separate pollen group.

The most comprehensive work on the morphology and phylogeny of the Acacia pollen was carried out by Ph. Guinet (1969) in his study of the Mimosaceae pollen. He described three types in the Acacias, the Australian, the fissured type of the Gummiferae (Group I), and the non-fissured type of the Vulgares (Group II and III) and the Filicinae (Central American). He treated A. albida as a separate type and insisted on transferring it to the Ingeae tribe under the monotypic genus Faidherbia.

The present results come close to those of Guinet but with some different conclusions especially as regards the Vulgares and Filicinae type of Guinet.

Materials and Methods

Most of the Acacia pollen was collected by me in the Sudan, bottled in acetic-alcohol (3:1) and kept in deep freeze. Other species which were not available at the time of collection were taken from dry herbarium materials from the Forest Department Herbarium in the Sudan or from the University of Khartoum collections.

The Acetolysis method of Erdtman was firstly tried but abandoned due to the tendency of the polyads to disintegrate and loose their natural compact arrangement which is necessary for this study. The method used was to put the flowers or buds in warm water to soften them and then transfer the anthers directly on to a slide with Gentian violet or Cotton blue glycerine jelly. A cover slip is put over the jelly and heated gently until the jelly melts and the cover slip is firmly resting on the slide. The pollen under the cover slip is then studied with a light microscope of

Plate 18. Acacia pollen. Type 1.

a. _A. seyal_ var. _seyal_ polyad (x 1000).

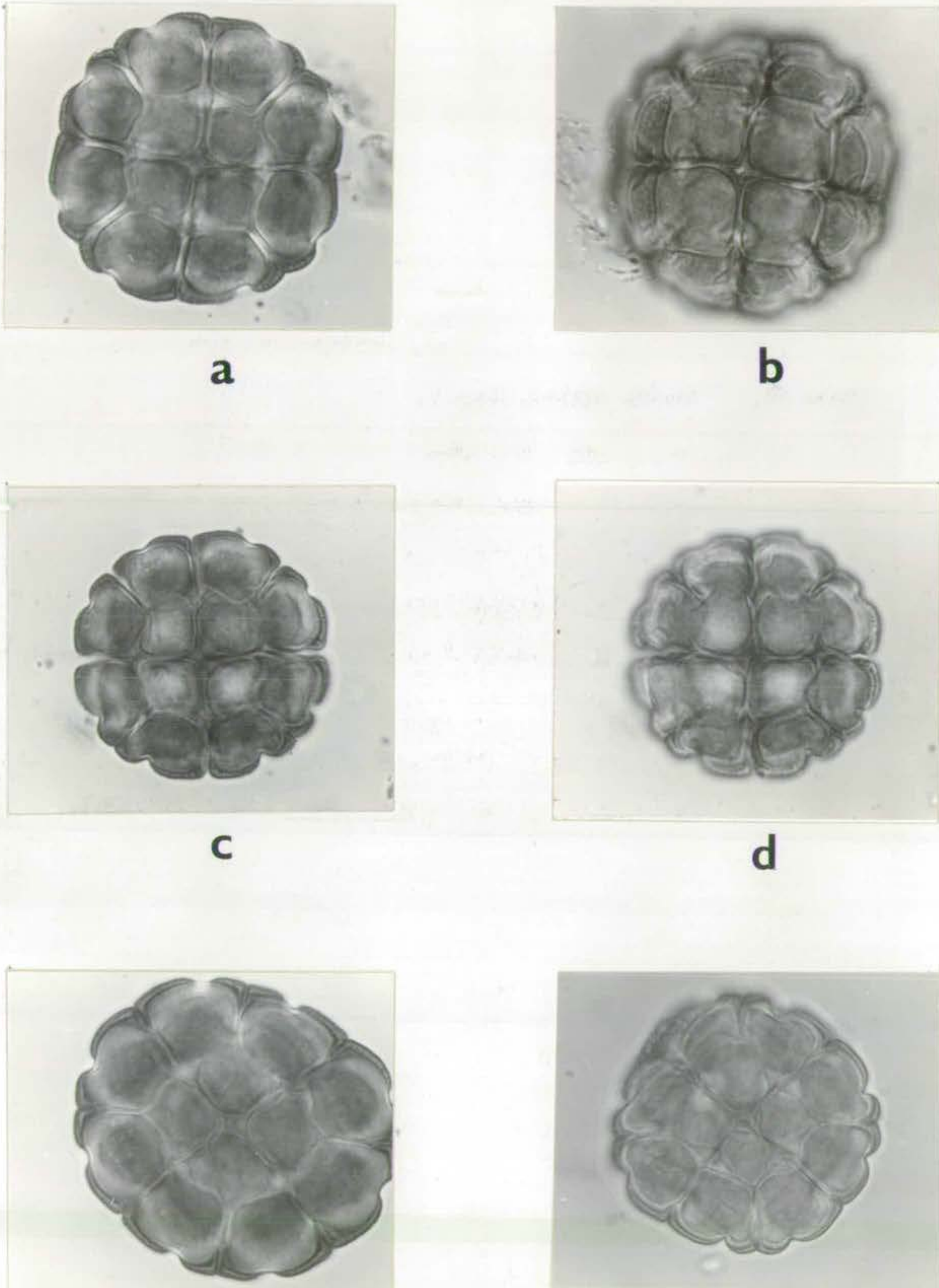
b. _A. seyal_ var. _seyal_ polyad (x 1000) showing central monads with three pores.

c. _A. dolichocephala_ polyad (x 1000).

d. _A. dolichocephala_ polyad (x 1000) showing central monads.

e. _A. gerrardii_ polyad (x 1000).

f. _A. tortilis_ subsp. _spirocarpa_ polyad (x 1000).



Pl.18

Plate 19. Acacia pollen. Type 1.

a. *A. nubica* polyad (x 1000).

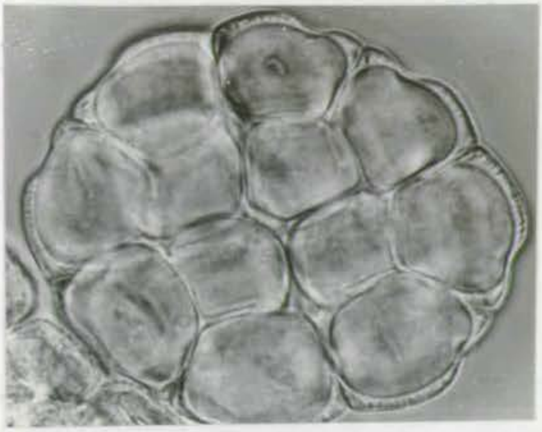
b. *A. macrothyrsa* polyad (x 1000).

c. *A. paolii* polyad (x 1000).

d. *A. tortilis* subsp. *raddiana* polyad (x 1000).

e. *A. horrida* subsp. *binadirensis* polyad (x 1000).

f. *A. lahai* polyad (x 1000).



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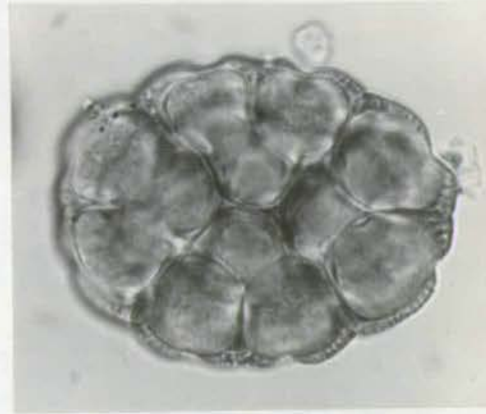

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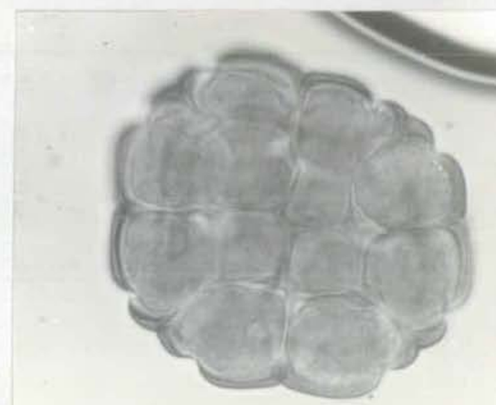


d

e

f

Pl.19

Plate 20. Acacia pollen. Type 2a.

a. <u>A. mellifera</u> subsp. <u>mellifera</u> polyad (x 1000).

b. <u>A. senegal</u> polyad (x 1000).

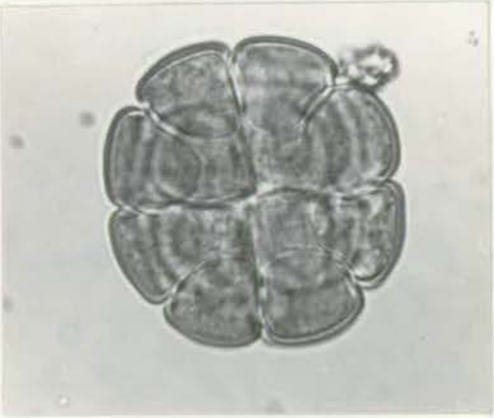
c. <u>A. macrostachya</u> polyad (x 1120) showing central monads.

d. <u>A. persiciflora</u> polyad (x 1120).

e. <u>A. polyacantha</u> subsp. <u>campylacantha</u> polyad (x 1000).

f. <u>A. laeta</u> polyad (x 1000) showing 20 monads, semi-distorted.

a



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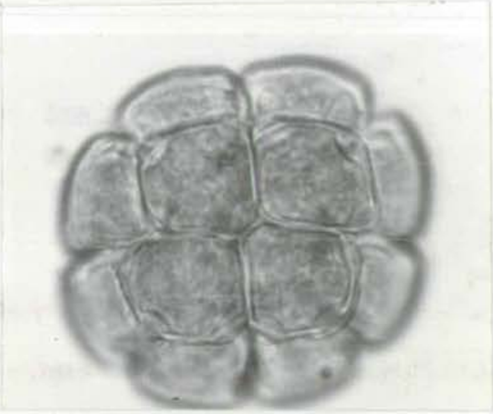

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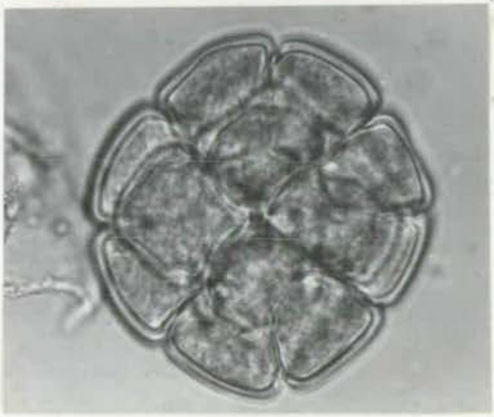

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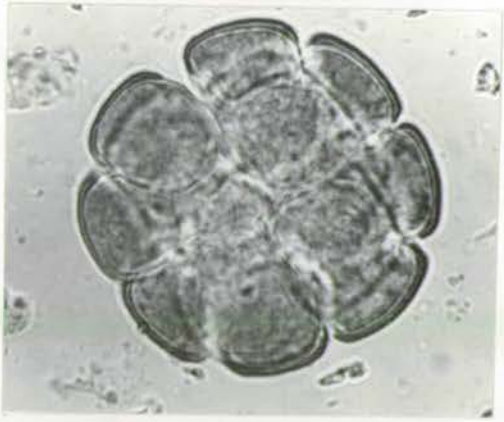

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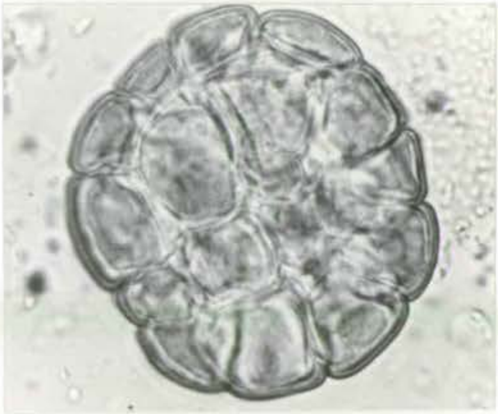


f

Pl.20

Plate 21. Acacia pollen. Type 2b and _A. albida_ type.

a. _A. pentagona_ polyad (x 1000).

b. _A. ataxacantha_ polyad (x 1000).

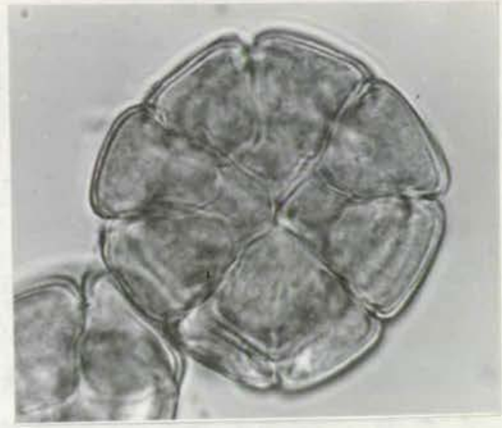
c. _A. schweinfurthii_ polyad (x 1000).

d. _A. albida_ polyad (x 525), 36-celled.

e. _A. albida_ (x 300). Two polyads inside anther sac.

f. _A. albida_ (x 1600). One monad showing 4 pores.

a



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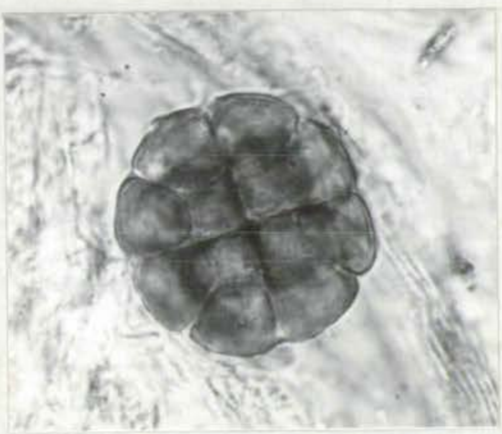

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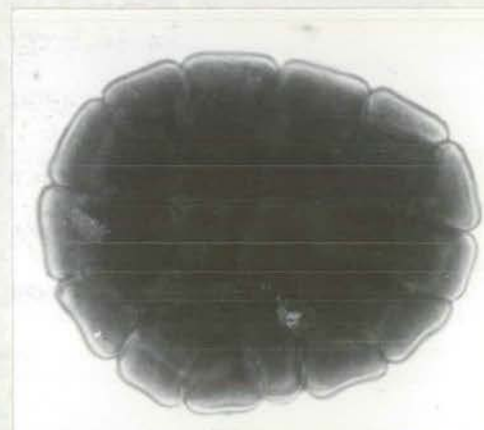

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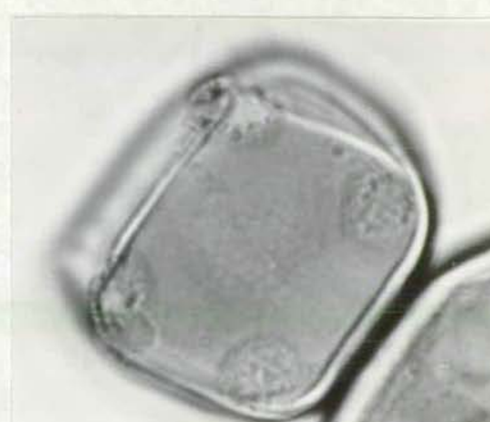


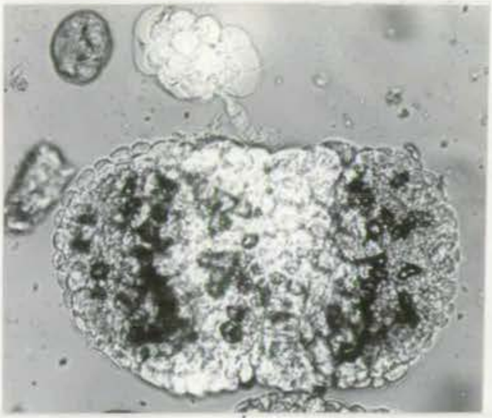
f

Pl. 21

Plate 22. Acacia anthers.

a. A. asak (x 280) anther with stipitate gland.

b. A. brevispica (x 250) anther with stipitate gland.



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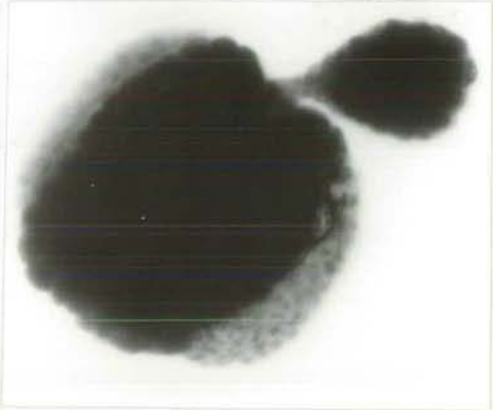


b

Pl. 22

x1000 magnifications. Photographs were taken of the polyads which gave reasonable results of the morphology of the polyads. (See Plates 18-22 pages 108-112).

Description of the pollen and anther characters

Acacia pollen and anther characters were investigated for the following characters:

Pollen:

Polyad:	Shape, size (length, width and thickness in μ) and the number of the monads in the polyad.
Central monads:	Length μ, structure of the exine and its shape.
Pores and fissures:	The number of pores, absence or presence of fissures and their number.
Baculae:	Presence or absence.

Anther:

Size:	Width is measured to give an idea of the size.
Stipitate gland on apex of anthers:	Presence or absence and its diameter μ.

The following is a tabular statement of the collected data on the Acacia pollen and anthers.

TABLE NO. 4 POLLEN AND ANTHER CHARACTERS OF THE SUDAN ACACIAS : L = length, W = width, Th = thickness

	Polyad								Exine				
Name	No. of monads	L	W	Th	Shape	No. of pores	No. of fissures	Length of central monad	Structure	Baculae	Outline broken or continuous	Anther sac width μ	Stipitate gland diam. μ
1. A. nubica	16	48	43	26	oval	3	3	11	psilate	+	broken	232	80
2. A. etbaica	16	40	40	27	circular	3	3	8	"	+	"	144	80
3. A. sieberana	16	53	53	27	"	3	3	16	"	+	"	480	96
4. A. gerrardii	16	56	48	44	oval	3	3	16	"	+	"	272	88
5. A. elatior	16	40	40	24	circular	3	3	8	"	+	"	248	80
6. A. reficiens	16	40	37	24	oval	3	3	8	"	+	"	160	80
7. A. paolii	16	43	37	24	"	3	3	11	"	+	"	184	112
8. A. kirkii	16	44	44	22	circular	3	3	8	"	+	"	162	80
9. A. hockii	16	40	37	24	oval	3	3	10	"	+	"	208	72
10. A. drepanolobium	16	43	37	32	"	3	3	9	"	+	"	280	120
11. A. ehrenbergiana	16	43	43	25	circular	3	3	13	"	+	"	200	96
12. A. tortilis ssp.tortilis	16	40	40	28	"	3	3	19	"	+	"	208	128
13. " ssp.raddiana	16	45	45	32	"	3	3	13	"	+	"	288	112
14. A. seyal	16	54	54	40	"	3	3	14	"	+	"	280	96
15. A. nilotica	16	43	43	19	"	3	3	13	"	+	"	224	88
16. A. macrothyrsa	16	56	44	48	oval	3	3	16	"	+	"	368	120
17. A. dolichocephala	16	40	40	27	circular	3	3	11	"	+	"	256	88
18. A. horrida	16	40	40	27	"	3	3	10	"	+	"	232	88
x19. A. lahai	16	41	41	28	"	3	3	10	"	+	"	230	88
20. A. mellifera	16	45	45	24	"	4	-	16	smooth	-	continuous	288	120
21. A. laeta	18-20	44	44	24	"	4	-	12	"	-	"	256	112
22. A. senegal	16	40	40	29	"	4	-	16	"	-	"	244	88
23. A. asak	16	38	35	19	oval	4	-	16	"	-	"	184	72
24. A. macrostachya	16	38	38	29	circular	4	-	13	"	-	"	256	80
25. A. hecatophylla	16	40	40	32	"	4	-	12	"	-	"	232	80
26. A. persiciflora	16	43	43	28	"	4	-	16	"	-	"	256	128
27. A. polyacantha	16	49	45	32	oval	4	-	16	"	-	"	240	80
28. A. ataxacantha	16	36	36	27	circular	4	-	16	"	-	"	160	64
29. A. brevispica	16	35	35	24	"	4	-	10	"	-	"	160	64
30. A. schweinfurthii	16	32	32	19	"	4	-	11	"	-	"	160	64
31. A. pentagona	16	32	32	24	"	4	-	11	"	-	"	160	64
32. A. albida	28-36	120	98	85	oval	4	-	29	areolate	+	"	592	absent

Table No. 5 showing the co-ordination of the two types of Acacia pollen as compared in the two groupings (inflorescence versus stipules) and the present Grouping (I-IV)

Name	Infl. Spic.	Infl. Cap.	Type 1	Type 2	Stipules Spinescent	Stipules non-Spinescent	Group
A. nubica		+	+		+		I
A. etbaica		+	+		+		I
A. sieberana		+	+		+		I
A. gerrardii		+	+		+		I
A. elatior		+	+		+		I
A. reficiens		+	+		+		I
A. paolii		+	+		+		I
A. kirkii		+	+		+		I
A. hockii		+	+		+		I
A. drepanolobium		+	+		+		I
A. ehrenbergiana		+	+		+		I
A. tortilis ssp. tortilis		+	+		+		I
A. tortilis ssp. raddiana		+	+		+		I
A. seyal var. seyal		+	+		+		I
A. seyal var. fistula		+	+		+		I
A. nilotica ssp. nilotica		+	+		+		I
A. nilotica ssp. tomentosa		+	+		+		I
A. nilotica ssp. astringens		+	+		+		I

Table No. 5(cont.)

Name	Infl. Spic.	Infl. Cap.	Type 1	Type 2	Stipules Spinescent	Stipules non-Spinescent	Group
A. macrothyrsa		+	+		+		I
A. abyssinica		+	+		+		I
A. dolichocephala	+		+		+		I
A. horrida	+		+		+		I
A. lahai	+		+		+		I
A. mellifera	+			+		+	II
A. laeta	+			+		+	II
A. senegal	+			+		+	II
A. asak	+			+		+	II
A. macrostachya	+			+		+	II
A. hecatophylla	+			+		+	II
A. persiciflora	+			+		+	II
A. polyacantha	+			+		+	II
A. ataxacantha	+			+		+	III
A. brevispica		+		+		+	III
A. schweinfurthii		+		+		+	III
A. pentagona		+		+		+	III
A. albida	+				+		IV

Summary and discussion

The Acacias are insect-pollinated species. Eight polyads are produced in the anthers with four polyads in each chamber. The polyads in the Sudan species consist of 16 monads (A. albida is exceptional) with eight monads arranged peripherally and four on each side of the polyad arranged centrally. The unit of the polyad is compact and does not separate easily. The shape of the polyad varies from oval to circular with the central monads usually having a square or rectangular shape; the peripheral monads can be square or triangular with rounded corners. The size of the polyad is variable in the different groups, from a length of 32-56 μ, width 32-54 μ and a thickness of 19-48 μ. A. albida has exceptionally large polyads with a length of 110-125 μ, width 96-110 μ, and its monad length is 29 μ compared with 8-16 μ in other Acacias. The anther in A. albida is 592 μ in width as compared with 160-368 μ in other Acacias. The exine structure of A. albida monads is areolate, a type found in the Ingeae but not in the Acacias where it is psilate or smooth. An important character which separates A. albida from the other Acacias is the absence of a stipitate gland in the apex of the anther. This character is found on all Acacia species of the Sudan.

The data in Table No. 5 page 119 separates the Acacias into two distinct groups (A. albida excluded) which are correlated perfectly well with the stipular characters.

The two types of pollen (see fig. page) are as follows:

Type 1		Type 2	
1. Polyad	L = 40-56 μ	1. Polyad	L = 32-49 μ
	W = 37-54 μ		W = 32-45 μ
	TH = 22-48 μ		TH = 19-32 μ

Type 1		Type 2	
2. Pores	= 3	2. Pores	= 4
3. Furrows	= 3	3. Furrows	absent
4. Baculae	present	4. Baculae	absent
5. Exine outline	broken	5. Exine outline	continuous
6. Exine structure	psilate	6. Exine structure	smooth
7. Anther width	= 160-480 μ	7. Anther width	= 160-288 μ
8. Stipitate gland D	= 80-128 μ	8. Stipitate gland D	= 64-120 μ

L = Length, W = Width, TH = Thickness and D = Diameter

Type 1 pollen is found in all members of Group 1. This group includes A. horrida and A. lahai (S. Africa), both with spicate inflorescence.

Type 2 pollen occurs in Groups II and III and the pollen can be subdivided into two groups, based on the size of the anther and polyads:

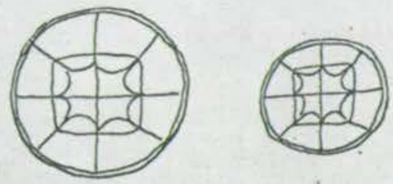
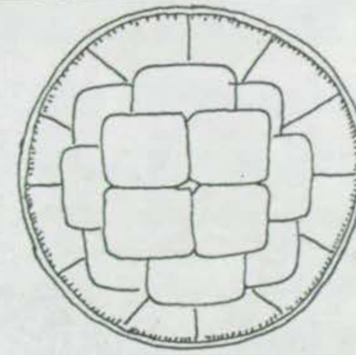
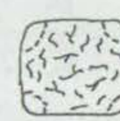
a) Pollen with short polyad diameter 32-36 μ, stipitate gland diameter 64 μ and anther width 160 μ .... Group III (climbers)

b) Pollen with polyad diameter $> 38 \mu$, stipitate gland diameter $> 80 \mu$, and anther diameter $> 184 \mu$ .... Group II

Type I pollen, which is found in Group I, contains the largest pollen grains; they are highly differentiated with furrows, baculae and a broken exine outline.

Type II a and b, which are represented by Groups II and III respectively, is smaller in size than Group I and is not differentiated, without furrows and baculae, and the exine outline is continuous. Types II a and b differ

FIG. 12 POLLEN TYPES

POLLEN TYPE 1	POLLEN TYPE 2(a,b)	A.ALBIDA POLLEN
	 a b	
Polyad type of Group 1	Polyad types of Groups 11 & 111	A.Albida polyad
CENTRAL MONAD TYPES:		
		
Round-angled triangular shape 3 pores 3 fissures Exine psilate Tectum broken	Rectangular-square shape 4 pores No fissures Exine psilate to smooth Tectum continuous	Rectangular-square shape 4 pores No fissures Exine areolate Tectum continuous
GROUP I	GROUP II and III	GROUP IV

from each other quantitatively but the qualitative characters are the same. The size of polyads and anthers is markedly smaller in Type II a than b.

A. albida is exceptional as its pollen characters qualitatively and quantitatively differ greatly from other Acacias.

To compare the results of this pollen investigation with the recent studies, it is evident that the results of my studies confirm but extend the grouping put forward by Guinet (1969). According to his work there are three types of pollen in the Acacia, the Vulgares type (Groups II and III), the Gummiferae type (Group I) and the Australian type. I have sub-divided Guinet's Vulgares type into two subdivisions, based on size differences only, type 2 a and b corresponding to Groups III and II respectively. Group I is represented in Guinet's work by the Gummiferae type, and we agree on the highly differentiated characters of this group. His Australian type is interesting in having different characters from the other Acacias; their pollen has 4 pores and 4 furrows, but in other pollen characters are more related to the Vulgares type (Type II) than the Gummiferae. This might support the view, which I share, that the Vulgares are ancestral, giving rise to the Australian group of Acacias in one direction and the Gummiferae in another direction.

Coetzee (1955) made a misinterpretation of the pollen results in her South African Acacias by dividing the Acacias into spicate and capitate groups before studying the pollen characters. Instead of judging the pollen characters on their merits, they were made to agree with the traditional inflorescence classification. As a result of this, she put both A. mellifera subsp. detinens (sub-globose infloresence but non-spinescent stipules) and

A. pennata (A. brevispica pro parte) (capitate inflorescence but non-spinescent stipules) with the capitate groups. The pollen types do not fit with that of the capitate group and so she put them in a separate third pollen group. In this work A. mellifera subsp. detinens and A. pennata will fit in type 2.

All the workers on the pollen types of Acacia agreed on separating A. albida as having a different pollen type from the others, and Guinet, after studying the Ingeae pollen decided to put A. albida in the Ingeae and retained the name Faidherbia for the monotypic genus.

Finally pollen morphology strongly reinforces the correlation already established between stipular types and the anatomy of prickles and spines; at the same time rejects the inflorescence classification.

The following synoptic key separates the 4 Acacia groups according to their pollen and anther characters in the Sudan:

1. Polyad of 16 cells; stipitate gland present on anther
  2. Pores 4, furrows absent, polyad outline continuous
    3. Polyad diameter = 32-36 μ, stipitate gland diameter = 72-128 μ .... Group II
    3. Polyad diameter = 32-36 μ, stipitate gland diameter = 64 μ .... Group III
  2. Pores 3, furrows 3, polyad outline broken .... Group I
1. Polyad of 28-36 cells; stipitate gland absent on anther .... Group IV

E. CYTOLOGY

Previous work

The first work on Acacia chromosomes was started by Ghimpu (1929-30); he dealt briefly with the distribution of polyploidy in Acacia and found that the Australian species with 2n = 26 have long chromosomes ranging up to 3μ, while the Asiatic, African and American species investigated by him had 2n = 52 and 104 and the chromosome length ranges up to 1μ. He pointed out the presence of somatic doubling or endoploidy and persistence of nucleoli till metaphase stages.

Newman (1934) worked on the Australian species A. baileyana and postulated that the haploid number of n = 13 was due to its being a secondary balanced polyploid, derived from a likely basic chromosome number 7 which on doubling was reduced to 13 with the fusion of a pair of chromosomes.

Senn (1938) reviewed the chromosome number relationship in the Leguminosae and concluded that more detailed investigations are needed in the Mimosaceae for a further understanding of its phyletic relationships. Castronova (1945) worked on 12 Acacia species and supported Ghimpu's findings, but concluded that the American Acacias are evolutionary, intermediate between the Australian and Afro-Asian species. His conclusion was based mainly on chromosome sizes as follows :

1. 2n = 26; chromosomes from 3μ in length...............Australian species
2. 2n = 26,52; chromosomes from $1\text{-}3\mu$ in length..........S. American species
3. 2n = 52, 104, 208; chromosomes 1μ in length..........Afro-Asian species

The variance in 2n number within a continental group does not refer to true polyploidy but to endopolyploidy.

Atchison (1948) determined the chromosome number of 19 species of Acacia, thus bringing the total of Acacias studied to 38 species. He strongly opposed the conclusion arrived at by Castronova (1945) as regards the intermediate evolutionary status of the American Acacias between the Australian and Afro-Asian species. Atchison instead postulated that the morphologically most primitive and very widely spread section, the Gummiferae (Group I), independently gave rise to the diploid Australian species, the diploid American species, and regarded Australia, Asia, Africa and America as secondary centres of speciation for Acacia. The same conclusion was arrived at by Andrew (1914) on the basis of morphological and geographical distribution and without any reference to cytological data.

M. I. Khan (1951) made a study of the somatic chromosomes in some diploid Acacia species ($2n = 26$) and their hybrids; he pointed out the presence of satellites and nucleoli during metaphase; he also noticed the smaller sizes of the Asian and African chromosomes as compared to those of the Australian species. He found that the hybrid between A. mollissima and A. decurvens has $2n = 26$, and between A. mellifera and A. senegal has $2n = 39$ (cf. A. laeta on page 228).

Sharma and Bahattacharya (1958) studied the structure and behaviour of Acacia chromosomes and noticed the gross morphological resemblance in the different species.

According to Darlington and Wylie (1961) and Fedorov (1969), the chromosome numbers of 57 species are known; most of them are Australian.

Materials and methods

Seeds of the Sudan Acacias were germinated (as mentioned before, page 59 in petri dishes or pots and put in a warm glass-house at a temperature of 75°F. They were allowed to grow for 2-3 weeks until they developed large healthy roots. Root tips were then taken from the fleshy white roots and put in Paradichlorobenzine (PDB) as a pretreatment before fixing. After 1-3 hours they were transferred to 3:1 acetic-alcohol fixative for a period of at least half an hour. They were then removed from the acetic-alcohol and put in normal HCl and placed in a water bath at 60°C for 5 minutes. The root tips were then removed for squashing, using lacto-acetic orcein as a stain.

This method was chosen after tedious trials with different methods of treatments, fixatives and stains, and gave the best possible results with Acacia chromosomes.

Leaf smears were also used and treated in the same manner as the root tips. Leaves were chosen from the growing buds at the apex of the growing shoots.

The prepared slides were then viewed under a high-powered microscope with phase contrast. The Swiss Weiss microscope was found to be most satisfactory for the purpose, and the phase contrast and the automatic camera were essential for the chromosome counts (see Pl.23,24 page 127 & 128).

Results

The study of the chromosome numbers of the Sudan Acacias presented great difficulties, due to the small size of the chromosomes (1μ or less), their high number (up to 104), cell intrusions (tannins and starch grains), and weak stainability. These difficulties were experienced before by all the previous workers and consequently no detailed study of the morphology of the chromosomes was attempted.

The following Table No. 6 gives the results of chromosomes counts of the Acacia species studied. Species marked with an asterisk have been counted here for the first time.

Table No. 6 Chromosome Numbers

* = species counted for the first time

Name of species	Number of chromosomes 2 n	Group	Spicate (S) Capitate (C)
A. seyal var. seyal	52	I	(C)
* " " fistula	52	I	(C)
*A. ehrenbergiana	52	I	(C)
A. nilotica subsp. nilotica	52,104	I	(C)
" " tomentosa	52,104	I	(C)
" " astringens	52	I	(C)
*A. drepanolobium	52	I	(C)
*A. nubica	52	I	(C)
A. sieberana	52	I	(C)
*A. gerrardii	52	I	(C)
A. tortilis subsp. tortilis	52	I	(C)
" " raddiana	52	I	(C)
*A. hockii	52	I	(C)
A. horrida	52	I	(S)
*A. paolii	26	I	(C)
*A. kirkii	26	I	(C)
*A. macrothyrsa	26	I	(C)
*A. elatior	26	I	(C)

Table No. 6 (cont.)

Name of species	Number of chromosomes 2n	Group	Spicate (S) Capitate (C)
*A. abyssinica	26	I	(C)
*A. dolichocephala	26	I	(sub-globose)
A. mellifera	26	II	(S)
A. laeta	39	II	(S)
A. senegal	26	II	(S)
A. polyacantha ssp. campylacantha	26	II	(S)
*A. asak	26	II	(S)
A. ataxacantha	26	III	(S)
*A. brevispica	26	III	(C)
*A. schweinfurthii	26	III	(C)
*A. kraussiana (S. Africa)	26	III	(C)
A. albida	26	IV	(S)

The above results show the occurrence of polyploidy in Group I only, and especially in the species which grow in northern and central parts of the Sudan, e.g. A. tortilis and A. ehrenbergiana in the north, A. gerrardii, A. nubica and A. seyal in Central Sudan. Diploid species occur in all the Acacia groups in central and southern parts of the Sudan. The results show that Southern Sudan has diploid species exclusively; conversely Northern Sudan has polyploid species exclusively. Central Sudan has a mixture of diploid and polyploid species. There is thus an apparent latitudinal relationship with polyploidy. Also the polyploids seem to be adapted and

Plate 23. Acacia chromosomes.

a. *A. seyal* var. *fistula* (x 2200) 2n = 52.

b. *A. nubica* (x 1800) 2n = 52.

c. *A. gerrardii* (x 2200) 2n = 52.

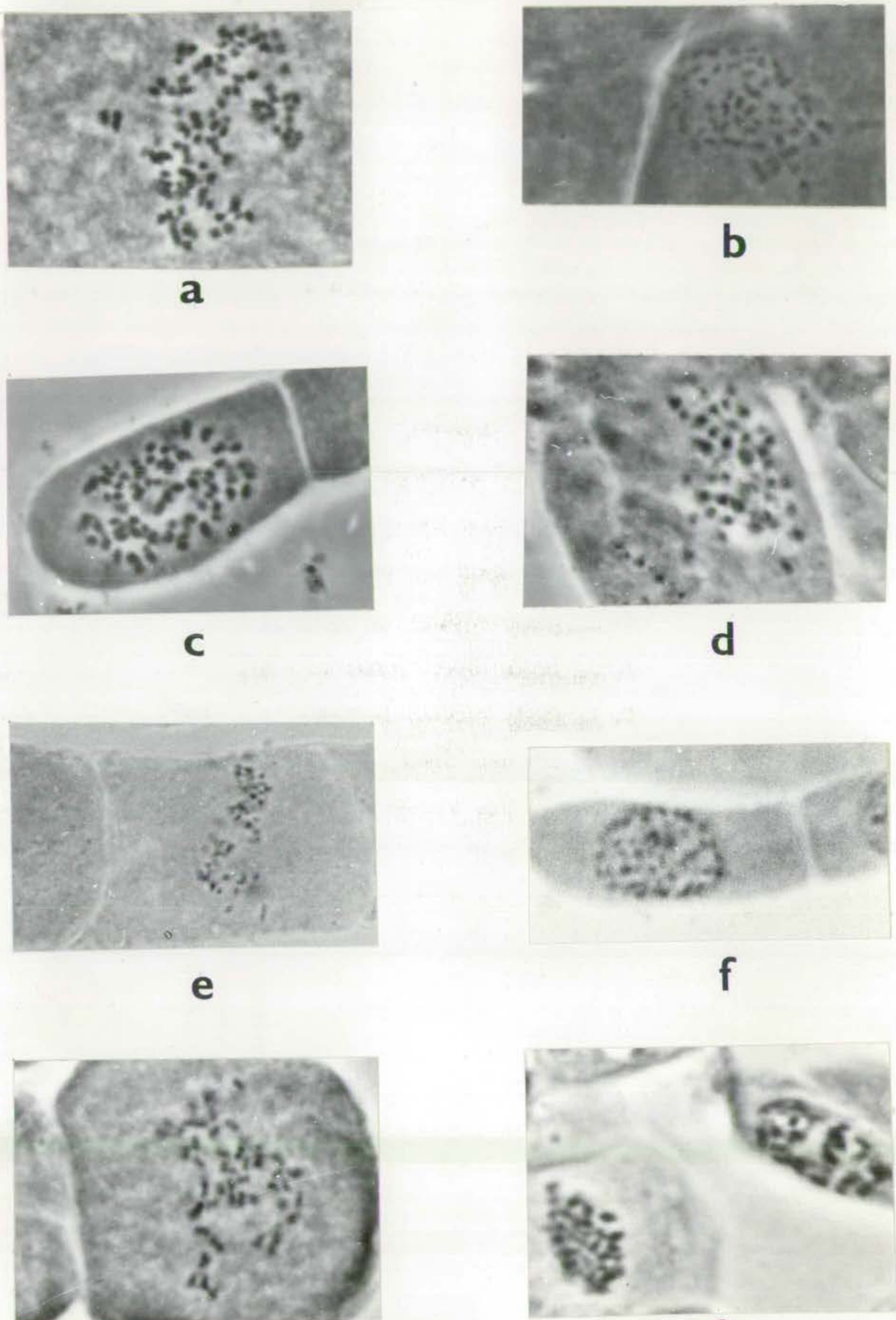
d. *A. drepanolobium* (x 2200) 2n = 52.

e. *A. sieberana* (x 2400) 2n = 52.

f. *A. ehrenbergiana* (x 2200) 2n = 52.

g. *A. nilotica* subsp. *nilotica* (x 2400) 2n = 52.

h. *A. elatior* (x 2800) 2n = 26.



Pl. 23

Plate 24. Acacia chromosomes.

a. A. senegal (x 2500) 2n = 26.

b. A. laeta (x 3600) 2n = 39.

c. A. ataxacantha (x 3300) 2n = 26.

d. A. schweinfurthii (x 2200) 2n = 26.

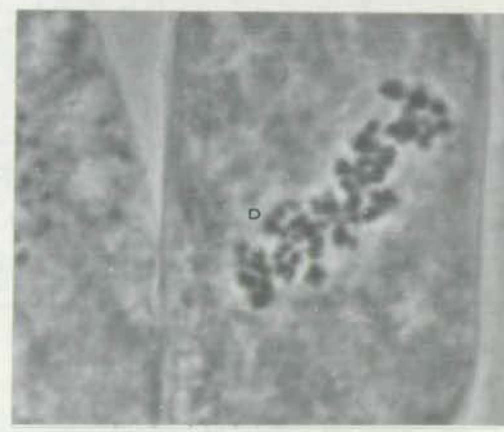
e. A. brevispica (x 2400) 2n = 26.

f. A. albida (x 3200) 2n = 26.

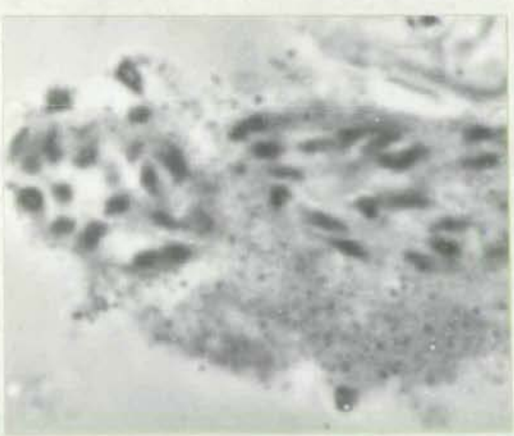
a

b

c



d



e

f

Pl. 24

survive well on dry arid zones of the Northern Sudan. Species of the Tobosa area, i.e. South-Eastern Sudan, have all diploids, though the area has a savanna grassland type, but it seems the aridity is not as extreme as it is in Northern Sudan. Thus it is apparent that none of the members of Groups II, III and IV is a polyploid. One exception is A. laeta of Group II, which is a triploid 2n = 39, but this species is suspected of having arisen through hybridisation between A. mellifera and A. senegal, and it is reasonable to treat its chromosome number as exceptional. According to this study A. albida has 2 = 26 and grows in all parts of the Sudan. However, a recent study by Halevy (1971) in Palestine revealed a polyploid A. albida, 2n = 52. This makes A. albida the only species known to contain both diploid and polyploid cytodemes.

There is no correlation at all between inflorescence type and chromosome number, as claimed by many recent workers. Spicate species can be diploid, as in all members of Group II, or polyploid as in A. horrida (Group I) and A. albida (Group IV), (Halevy 1971); the capitate species can also be diploid or polyploid. Though there is no well defined correlation between stipular types and chromosome numbers, all polyploid species have spinescent stipules. Polyploidy is absent in the non-spinescent stipulate species of Groups II and III that have been counted.

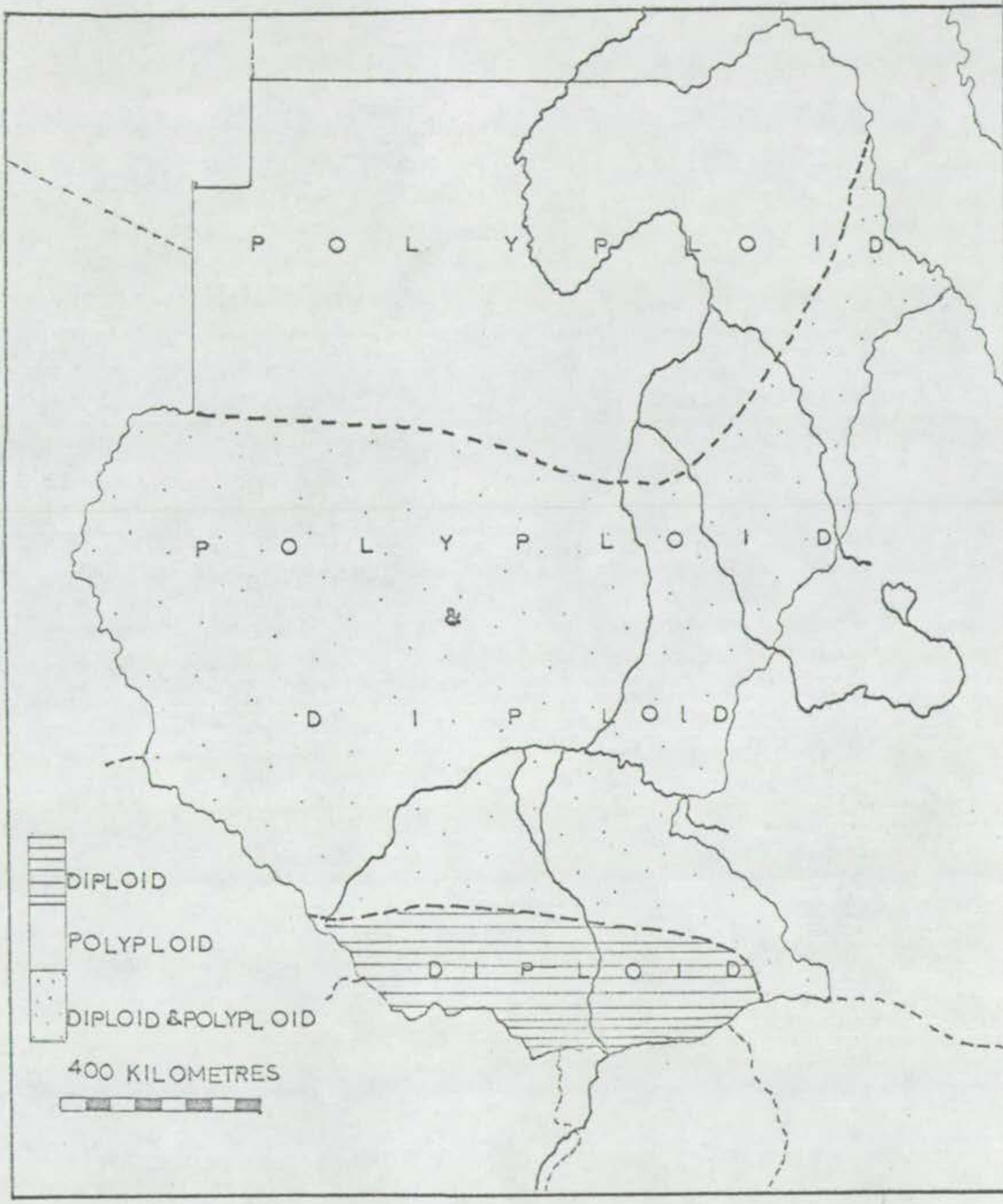
An attempt was made to measure the chromosome size, but is considered unreliable due to the unevenness of the sections and the consequently variable positions at which the chromosomes are lying on the sections. Yet generally it was noticed that the chromosomes of the polyploid species are smaller than the diploid ones. The grouping made on the basis of chromosome sizes by Ghimpu (1929) and Castronova (1945) was rejected and criticised by Atchison (1948) who stated "Variations in chromosome size, especially among the very small chromosomes of Acacia, cannot be given great significance. The optical functions of the instruments and individuals are not consistent enough for accurate comparisons among authors". I tend to agree with Atchison's conclusions regarding the size of the Acacia chromosomes and its taxonomic significance; this will be discussed later when the overall attributes collected in this study are discussed.

Endopolyploidy exists in Acacia species and has been reported by Ghimpu (1929). In this study I have noticed this phenomenon in A. nilotica, where in the same root tip I found cells with different number of chromosomes, 52 and 104. The cause of this phenomenon is not clear, though Atchison (1948) attributes it to nitrogen fixing nodules or the results of leptohormones from wounds. Atchison also reported the presence of endopolyploidy after pretreatment with Colchicine or Paradichlorobenzene. This phenomenon seems to be restricted to Group I amongst the polyploid species.

In this work new counts are presented for 16 species. There are no counts for the following Sudan species, A. hecatophylla, A. persiciflora, A. macrostachya and A. reficiens, due to the absence or failure of their seeds to germinate. The cytological results on Group III, the climbers, are completely new and add further evidence in favour of their homogeneity as a separate group within the genus.

It is remarkable to note that polyploidy is absent in the Australian Acacias, very rare in the American species and common in the African and Asian species.

Atchison in his study of the cyto-geography of the Acacias (1948) stated that "Polyploid Acacias do not have a more northern distribution, nor a wider dispersal, than the diploids". My results contradict this statement, because as regards the Sudan species, the polyploids are of northern distribution (see Map No. 4 page 132) and definitely have a wider distribution than the diploids (see Distribution Maps No. 5-43, pages 212-221).



MAP 4. DISTRIBUTION OF DIPLOID AND POLYPLOID ACACIAS IN THE SUDAN. (A. ALBIDA EXCLUDED)

III TAXONOMIC ACCOUNT OF THE SUDAN ACACIAS

1. INTRODUCTION

Most of the Acacia specimens studied in this work were collected by the writer in the field in different parts of the Sudan. The ecological habitats, vegetation types and distribution of Acacias were observed during the time of collection or during other treks while doing forestry work in the field. Specimens of the same species were collected from different localities to give a full range of the variations of the species.

The Acacia specimens preserved at the Sudan Forest Herbarium and the Herbarium of University of Khartoum were examined and compared with the field specimens.

The types were studied at Kew Herbarium and the British Museum, together with all the Sudan collections in the two herbaria. Specimens of Acacias in the Edinburgh Herbarium were also examined.

In all, about 880 herbarium specimens were studied from my own Sudan collections and the other herbaria, in addition to 200 samples of pods and seeds collected separately from different parts of the Sudan. Thus about 1000 specimens of Sudan Acacias were actually examined during the course of this study. Morphological studies were carried out on all the specimens and the species were described, giving the range of variations found in the different locations. Brenan's studies on the Acacias in F.T.E.A. (1959) and Fl. Zam. (1970) were frequently referred to, together with Ross's work on South African species, especially as regards the nomenclature and synonyms which were perfectly covered by both workers. The infraspecific categories used here are largely those of Brenan (1959).

A key for the identification of the Sudan Acacias is given after this introduction, followed by a descriptive account of the Sudan specimens.

Known Arabic names are mentioned after the Latin names of the species in brackets. The type specimen is mentioned with a mark (Herbarium !) if seen, and without ! if not actually seen by me. The synonyms are reduced to those concerning the Sudan species and especially as those mentioned in the Sudan floras. The description of the species covers practically all the ranges of variations in the specimens which I have examined. The ecological habitat is then mentioned, together with the geographical distribution in the Sudan. Distribution of the species in Africa is given in brackets after the Sudan distribution. Selected specimens were mentioned at the end of the account for every species and I have recorded these specimens according to their localities from the northern to the southern provinces. The choice of the specimens is arbitrary as it is impossible to put in all the specimens seen during this study, but an attempt was made to give representative specimens from different localities.

There are so far 31 species of Acacia native in the Sudan. I have added two records to the previous list of 29 (Jackson 1966), namely A. pentagona (from the British Museum) and A. kirkii (from Kew Herbarium). The former is a climber found in the moist regions of Southern Sudan, and the latter a tree, also found in Southern Sudan. As regards A. venosa Benth., described by Andrews in Fl. Pl. Sudan 2:133 (1952), I could not find a single record collected in the Sudan. The type specimen of this species collected and described by Schweinfurth is from Ethiopia and it is very difficult to distinguish the type from A. asak and A. senegal, being intermediate morphologically between them. Thus I found there is no evidence to justify the inclusion of A. venosa in the Sudan Flora. There are two other species of Acacias in the Sudan, namely A. farnesiana and A. mearsnii, but they are not included in this study as they are both known to be introduced in cultivation by the Forestry Department.

At Kew Herbarium I found a new species of Acacia collected by I. R. Dale No. 5303, 1943, in S. East Equatoria Province at Lorienatum and determined as A. Sp. Nov? This specimen is in the East African Herbarium in Nairobi and I saw only a photo of it at Kew (Kew, Negative No. 3267). The species have broad big leaflets like A. mellifera but with more than 4 pinnae, no pods or inflorescence were seen, and it is difficult to relate it to any of the existing species. A more comprehensive study of it is needed in the field before giving it any name.

2. KEY TO SUDAN ACACIAS

1. Stipules not spinescent; pod venation horizontal
  2. Prickles in pairs or threes at nodes, rarely a few also scattered in internodes; shrubs and trees
    3. Prickles in pairs
      4. Pinnae 2-3 paired
        5. Pinnae 2 paired; leaflets 1 pair .... 19. mellifera
        5. Pinnae 2-3 paired; leaflets 2-5 paired .... 20. laeta
      4. Pinnae more than 3 paired
        6. White hairs on rachis; prickles rarely on internodes
          7. Leaflets glabrous, apex obtuse, lateral nerves visible .... 21. hecatophylla
          7. Leaflets ciliolate, apex acute, lateral nerves not visible .... 22. polyacantha
        6. Golden hairs on rachis; no prickles on internodes
          8. Pod apex hooked; flower white-cream .... 23. macrostachya
          8. Pod apex obtuse; flower red or purple .... 24. persiciflora
    3. Prickles in threes
      9. Pod dark brown or pink, coriaceous .... 25. asak
      9. Pod straw-coloured, membranous .... 26. senegal
  2. Prickles many, scattered on internodes; climbers
    10. Inflorescence spicate .... 27. ataxacantha
    10. Inflorescence capitate
      11. Petiole less than 1.6 cm long .... 28. brevispica
      11. Petiole more than 1.6 cm long
        12. Branches olive-green or pale brown; pods and seeds flattened .... 29. schweinfurthii

12. Branches red-brown or purplish; pods and seeds not flattened .... 30. pentagona

1 . Stipules spinescent; pod venation longitudinal, oblique or not apparent

13. Inflorescence a globose (capitate) or sub-globose head

14. Inflorescence a globose (capitate) head

15. Flowers white

16. Pods straight, margin entire

17. Trees, branching from the one main stem

18. Pods woody or pulpy, thick, 8-21 x 1.5-3.5 cm .... 1. sieberana

18. Pods not woody nor pulpy, thin, 3-12 x 1-2 cm

19. Spines up to 3.5 cm long, not inflated .... 2. abyssinica

19. Spines up to 9 cm long, sometimes inflated .... 3. elatior

17. Shrubs, branching from base

20. Spines hooked .... 4. reficiens

20. Spines straight

21. Pods flattened, margin entire, glabrous; anthers green to yellow .... 5. etbaica

21. Pods not flattened wing-like, pubescent, anthers red .... 6. nubica

16. Pods spiral or falcate, margin constricted or undulating

22. Pods spiral, olive-green; spines both straight and hooked in the same plant .... 7. tortilis

22. Pods falcate, brown; spines all straight

23. Spines inflated; pods glabrous .... 8. _drepanolobium_

23. Spines not inflated; pods pubescent

24. Trees, one stemmed; bark black; leaves dark green; seeds compressed .... 9. _gerrardii_

24. Shrubs, many stems; bark green; leaves pale green; seeds not compressed .... 10. _paolii_

15. Flowers orange and yellow

25. Flowers orange; spines falcate, grey to brown . 11. _macrothyrsa_

25. Flowers yellow; spines straight and not falcate, white

26. Pods falcate, less than 0.9 cm wide

27. Trees, 1 or 2 stemmed; pinnae pairs more than 3; spines shorter than leaf length

28. Bark powdery, green or red; branches glabrous; spines 4-10 cm long, white, sometimes inflated; involucel on lower half of peduncle .... 12. _seyal_

28. Bark not powdery, yellow to brown; branches pubescent; spines short, 1.5 cm long, hardly up to 4 cm long, yellow to pale brown, not inflated; involucel on upper half of peduncle .... 13. _hockii_

27. Shrubs, many stemmed; pinnae pairs never exceeding 4 pairs; spines longer than leaf length 14. _ehrenbergiana_

26. Pods straight, more than 0.9 cm wide, necklace-shaped

29. Pods grey-black, pulpy, venation longitudinal or not apparent; longitudinal ridges on pod surface, corolla yellow .... 15. _nilotica_

29. Pods brown, venation radial, not pulpy; no ridges on pods surface, corolla red .... 16. kirkii

14. Inflorescence a sub-globose head.................... 17. dolichocephala

13. Inflorescence a cylindrical spike

30. Shrubs; pod brown, falcate; anthers glandular .... 18. horrida

30. Trees; pod orange, coiled or spiral; anthers eglandular 31. albida

1. A. SIEBERANA DC., Prodr. 2:463 (1825).

Arabic: Kuk.

Type: Senegal, Sieber (K, iso!).

Tree 5-20 m high, bark usually yellowish grey, smooth yellowish or rough fissured grey, sometimes light brown and flaking on branches. Young branches glabrous to tomentose, green, grey or yellowish, turning later to grey. Stipules spinescent, glabrous, white, straight, 9-12 cm long (longest among the Sudan Acacias). Prickles and inflated spines absent. Leaves 3-14 cm long; petiole glandular, pubescent, 13 mm long; rachis 4-12.1 cm long, channelled adaxially, pubescent, glandular at end 2-3 pinnae, pinnae 6-17 pairs, 3-4.5 cm long, pubescent; leaflets (14-)16-17(-52) paired, linear-oblong, apex obtuse or subacute, glabrous or pubescent, margin ciliolate, midrib visible on both sides. Inflorescence in globose heads, white to cream-flowered, peduncle pubescent, 1-4 cm long, involucel pubescent, brown on top part of the peduncle; floral bracts brown stalked, white, hairy tipped, 1.8 mm long. Calyx pubescent, 2 x 0.5 mm, lobe tips pale. Corolla glabrous, white, 3.5 x 0.5 mm. Anthers white-creamy, 6 mm long, glandular. Ovary hairy, 1 mm long; stipe short, 0.2 mm long; style 4.5 mm long. Pod woody or pulpy, dark brown to pale grey, glabrous or pubescent, straight or slightly falcate, indehiscent, venation longitudinal, sometimes not apparent, 20 x 1-2.5 cm. Seeds olive to olive-brown or grey, oblong, 10-12 mm x 7.5-9 mm; areole marginal, closed or U-shaped, 10 x 6-6.5 mm; funicle 3 mm long, seeds lie vertically inside the pod. Flowering October-January; fruiting January to April.

Key to varieties :

1. Young branchlets glabrous or nearly so, branches of crown usually ascending .... var. sieberana

1. Young branchlets hairy, usually densely so, branches of crown usually widely spreading

   2. Leaflets 3-6 mm long; pods dark brown; bark light grey, smooth, alluvial sites .... var. vermoesenii

   2. Leaflets 2-2.5 mm long; pods light grey; bark dark brown to black, roughly fissured .... var. villosa

var. sieberana;Brenan, Fl. Trop. East Afr. 127 (1959).

Syn: A. verugera Schweinfurth in Linnaea 35:340 (1867-8).

Habitat: Deciduous woodlands and riverine forests on light silty soils.

Distribution: Southern parts of Central Sudan, i.e. south of Kordofan, Darfur and Blue Nile provinces and extending southwards along the Nile and its tributaries in the three southern provinces. (Also found in Ethiopia, Kenya, Uganda, Tanganyika, Rhodesia and Portuguese East Africa, westwards to Senegal, Nigeria, Cameroun, Ghana, Congo and Angola.)

Selected specimens: Blue Nile province, Singa, 1969, Elamin 425. Bahr Elghazal, Wau, 1969, Latif 321. Kassala, Red Sea Hills, 1960, Kassas E1000. Darfur Radom, 1969, Elamin 1572. Khartoum, Soba, 1969, Elamin 345.

var. vermoesenii (De Wild.) Keay & Brenan in Kew Bull. 1950:364 (1951).

Syn: Inga nefasia [Hochst. ex] A. Rich., Tent. Fl. Abyss. 1:237 (1847).

A. vermoesenii De Wild., Pl. Bequaert. 3:69 (1925).

Habitat: Riverine woodlands on light silty soils.

Distribution: South-West Darfur Province, River Ada and other banks of seasonal rivers. Also around Jebel Marra along watercourses. (In Africa found in East Africa, southwards to the Rhodesias and Portuguese East Africa and westwards to Ghana and Nigeria.)

Selected specimens: Darfur province, J. Marra, Beldong, 1964, Wickens 2159; Kalikoting, 1957, Francis 24; Nyrtete, 1964, Wickens 1347; Zalingi, 1964, Wickens 2835; Ada River, 1969, Elamin 1592.

var. villosa A. Chev. in Bull. Soc. Bot. Fr. 74.959 (1928).

Syn: A. rehmaniana Hutch & Dalz. in Fl. West. Trop. Afr., 1:360-361 (1927).

Habitat: Riverine sites on hilly slopes, 5500-6000'.

Distribution: Darfur, Jebel Marra at Golol and Beldong. (Also found in West Africa.)

Specimens seen: Darfur province, J. Marra, Golol, 1969, Elamin 1532. Khartoum, Khartoum Botanic Garden, 1969, Elamin 1414 (cultivated).

Observations: The three varieties occur in different habitats in the Sudan. Var. sieberana always grows along banks of permanent rivers and actually replaces A. nilotica on the White Nile banks in the three southern provinces; its crown is big and round with ascending branches which are usually glabrous. The other two varieties, vermoesenii and villosa, differ sharply in habitat and crown form; they both grow along seasonal watercourses and both have a spreading crown with pubescent spreading branches, and are separated as in the key by their leaflets, pods and bark characters. However, one specimen (Elamin 1414), which I collected at Khartoum Botanic Garden, has golden villous hairs, a character existing in a variant described by Keay and Brenan as var. woodii, but according to their distribution of this variety, it is limited to Natal, Transvaal, Northern Rhodesia and Angola and does not seem to extend as far north as the Sudan. Unfortunately, I could not establish the local origin of the specimen (which lacks pods) and consequently I have to place it with var. villosa on basis of the length of its leaflets and the low number of its pinnae which are usually more than 17 pairs in var. vermoesenii.

The treatment of A. sieberana variants is similar to that used in dividing the infraspecific variants of A. tortilis, in that it depends on differences in indumentum and habit. It may well be that subspecific rank should be accorded to the variants of A. sieberana as it was by Brenan in Fl. Trop. East Africa (1959) to those of A. tortilis.

2. A. ABYSSINICA (Hochst. ex) Benth. subsp. CALOPHYLLA Brenan in Kew Bull. 1957:82 (1957).

Type: Kenya, S. Kavirendo District, Mugunga, Greenway 7860 (K, holo, E.A. iso).

Syn: A. xiphocarpa [Hochst. ex] Benth. in Hook Lond. Journ. 96 (1842); Andrews, Fl. Pl. Sudan 2:148 (1952).

Tree 6-20 m high, flat crown. Main stem from base then forking at same level into branches which rise steeply to the same height. Bark brown-grey, fissured, on young branches papery. Branchlets pubescent to villous. Stipules spinescent. Spines brownish-white, straight, pubescent, 3-4.5 cm long. Leaves 7-10 cm long, glandular. Petiole 2-5 mm long, pubescent, glandular. Rachis 7-9.5 cm long, glandular, grooved adaxially, pubescent. Pinna very closely set, 15-36 paired, 0.4-1.5 cm long. Leaflets also closely set, 20-40 paired, 2 x 0.5 mm glabrous, margin not ciliolate, apex acute, midrib visible adaxially. Inflorescence in globose heads; peduncle pubescent 0.8-1.3 cm long; involucel in lower half of peduncle. Flower red, sessile. Calyx red, pubescent 1.5 x 0.7 mm. Corolla red, pubescent. Stamens free, glandular, 5 mm long; anther red. Ovary brown, 1 mm long; style 3.5 mm long; stipe 1 mm long. Pods grey-brown, straight, compressed, pubescent, venation longitudinal, 5-12 x 1.2-3.8 cm. Seeds lie obliquely in the pod, olive-brown, elliptic, compressed, 7-9 x 4.5 mm; areole U-shaped, marginal, 6-7 x 3 mm; funicle 3 mm long.

Habitat: On hills up to 1666 m in wooded grassland.

Distribution: Equatoria Province, Imatong and Didinga Mountains . (Also in Uganda, Tanganyika, Kenya, Congo, Portuguese East Africa, Nyasaland and S. Rhodesia.)

Selected Specimens: Equatoria, Katire 1970, Claudio 2; Didinga Mts., 1929, Chipp 55; Nagishot, 1939, Myers 11147.

3. A. ELATIOR Brenan subsp. TURKANAE Brenan in Kew Bull. 1957; 95 (1957).

Type: Kenya, Lodwar, Hemming 2970 (K, holo).

Large tree 18-25 m high. Bark brown to almost black, deeply fissured. Branchlets grey, densely pubescent with spreading hairs. Stipules spinescent and sometimes inflated. Spines pubescent, straight, 7-9 cm long. Leaves 6.5 cm long. Petiole 0.8-1 cm long. Rachis densely pubescent. Pinnae 5-13 pairs, 3 cm long. Leaflets 11-25 pairs, dark green, midrib visible on both sides, margin ciliolate, apex round, 3-4 x 1.25 mm. Inflorescence globose heads, white-creamy peduncle densely pubescent, 2-5 cm long, involucel on lower half of peduncle. Calyx pubescent, 1.5 x 0.5 mm. Corolla 2.5 x 0.5 mm. Stamens free, glandular, 5 mm long. Ovary 1 mm long, style 2 mm long and stipe 0.1 mm long. Pods straight, oblong, flattened, dehiscent, pubescent near base, venation longitudinal, margin not constricted, 10 x 1.2-1.8 cm. Seeds lie longitudinally or obliquely inside the pod; olive-brown, smooth, orbicular, compressed, 7 x 6 mm; areole U-shaped, marginal, 3-5 x 3.5-4 mm, the U-shaped areole is almost closing; funicle 3 mm long.

Habitat: Sandy river banks in dry savanna.

Distribution: South-East corner of Equatoria. (Also in Kenya and Uganda.)

Specimen seen: Equatoria, Kapoeta, 1939, Myers 10421.

Observation: The inflated spines which sometimes occur in this species and also in A. horrida are elongated at the base and very distinct from those of A. seyal var. fistula and A. drepanolobium where in the latter two the inflated spines are swollen like a ball (ant-galls).

4. A. REFICIENS Wawra subsp. MISERA (Vatke) Brenan in Kew Bull. 1957:90 (1957).

Type: Somaliland, Meid, 1875, Hildbrandt 1394 (K, iso!).

Syn: Acacia misera Vatbe in Oesterr. Bot. Zeitchr. 30:275 (1880).

Shrub 1-4 m high, obconical, branching from base. Bark grey. Branchlets grey, glabrous to pubescent. Stipules spinescent. Spines short, brown, all hooked (like A. tortilis), 0.3 mm long. Leaves small, 1.5 cm long. Petiole 0.4 cm long. Pinnae 2-4 paired. Leaflets 6-8 paired, 4 x 1 mm, glabrous or slightly puberulous, apex subacute. Inflorescence in globose heads; peduncle short, pubescent, 0.8-1.2 cm; involucel in lower half of peduncle. Flower sessile, white to cream. Calyx small, 0.8 x 0.2 mm. Corolla 3 x 0.5 mm. Stamens 5.5 mm long, glandular and free. Ovary 0.8 mm long; style 4 mm long; stipe 2 mm long. Pods straight, linear oblong, dehiscent, dark brown, glabrous, venation longitudinal, 5 x 0.7 cm. Seeds lie longitudinally in pods, olive-brown to green, elliptic, compressed, 5-7.5 x 4-5 mm; areole U to V-shaped, marginal; funicle dark brown, 3 mm long.

Habitat: Silty alkaline soils on banks of rivers in open savanna.

Distribution: South-East Equatoria province. (Also found in Uganda, Kenya and Somalia.)

Selected specimens: Equatoria, 1941, Myers 14000; Kapoeta, 1940, Myers 13437; 1953, Padva 221

Observation: The spines are brown and hooked like the A. tortilis group but differ in the absence of white long spines which are present in two subsp. of A. tortilis.

5. A. ETBAICA Schweinfurth subsp. ETBAICA; Brenan in Kew Bull. 1957:90 (1957).

Arabic: Arrad.

Type: Sudan, Red Sea Hills, Soturba Mts., 1864, Schweinfurth 1994, 1995.

Shrub to small tree, 2.4-12 m high; main stem with flat or round thick crown. Bark rough fissured, grey or dark brown to black. Branchlets red-brown, pubescent. Stipules spinescent, straight, frequently long, 0.5-2.5 cm long with few short ones, sometimes absent. Leaves pubescent, 2.8 cm long, glandular on petiole and at end 1-2 pinnae. Pinnae 4-6 paired. Leaflets 10-30 paired, oblong, glabrous, apex obtuse, midrib visible at adaxial surface, margin ciliolate, 2.5 x 0.5 mm. Inflorescence in globose heads, white to cream; peduncle pubescent, 0.7-2 cm long, involucel on the lower half of the peduncle; floral bract very small and brown. Hermophrodite and male flowers occur in the same capitulum. Calyx brown, 0.7 x 0.3 mm, pubescent tipped. Corolla 5-7 lobed, brown tipped, glabrous, 2.5 x 0.6 mm. Anthers free, glandular, red. Ovary sessile brown. Pods straight, linear-oblong to oblong, brown, dehiscent with attenuate base and accuminate to round apex, 2-6 x 0.5-2 cm; venation longitudinal. Seeds lie longitudinally inside pods; sub-circular, smooth, 8 mm diam.; areole U-shaped and marginal. Flowering in August, fruiting in March-April.

Habitat: Dry savanna at foot of hills.

Distribution: Kassala Prov., Red Sea Hills and also in the dry savanna in South-West Equatoria in Kapoeta. (Elsewhere in Africa it is reported only from Asmara in Ethiopia.)

Selected specimens: Northern Province, Nubia, 1865, Schweinfurth 1993. Kassala, Red Sea Hills, Soturba, 1864, Schweinfurth 1994 and 1995; Karora Hills, 1923, Crowfoot s.n.; Erkwit, 1932, Aylmer 233.

Observation: A. etbaica subsp. etbaica is only found on the Red Sea Hills associated in its southern distribution with A. asak and forms a vegetation type in the dry savanna zone. Its pods are related to the southern species, e.g. A. reficiens, A. elatior and A. abyssinica

6. <u>A. NUBICA</u> Benth. in Lond. Journ. Bot. 1:498 (1842).

Arabic: Laot.

Type: Sudan, Kordofan, 1842, <u>Kotschy</u> 407 (K, holo!).

Syn: [<u>A. orfota</u> auct. plur. non (Forsk) Schweinfurth]

Shrub 1-5 m high. Crown obconical, branches from base. Bark smooth green-grey or whitish green. Young branches pubescent, green, grey or grey-brownish. Stipules spinescent. Spines straight, pubescent, white with brown tips, 0.4-2 cm long. Leaf 1.5-8.8 cm. Petiole 0.4-1.3 cm long, pubescent, glandular. Rachis 1.5-7.5 cm long, pubescent, glandular, adaxially channelled. Pinnae 5-11 paired, 1.5-1.8 cm long. Leaflets 5-15 paired, 2.5-6 x 0.5-2 mm, ciliolate, apex acute to subacute. Inflorescence in globose heads; peduncle pubescent, 0.5-1.5 cm long, involucel on lower half of peduncle; floral bract white to cream, spook-like, 2 mm long, lobe 0.5 mm wide. Calyx 5-6 lobed, pink and green tipped, pubescent, 2 x 0.5 mm. Corolla 6-8 lobed, pink, green tipped, glabrous, 3 x 0.3 mm. Stamens free, 5 mm long, anthers red. Ovary brown, glabrous, 1 mm long; style 4.5 mm long; stipe 1 mm long. Pods straight, coriaceous, dehiscent, yellow or straw-colour, 4-12 x 1.2 cm, pubescent, apex obtuse, margin flattened into wing-like projections, venation longitudinal. Pod is divided into distinct septae but without any constrictions along the margins. Seeds 10-12 to the pod, globose, grey to olive-grey, 5-6 x 4-5 mm, surface wrinkled and they lie longitudinally or obliquely in the pod; areole circular, closed, marginal; funicle dark brown, 5.5 mm long. Flowering November-January; fruiting January-May.

<u>Habitat</u>: Semi-desert or dry savanna woodlands on dry hard clays; it also appears on denuded and over cultivated clay fields.

<u>Distribution</u>: Central and Northern Sudan. (Also in North-East Africa

from Egypt southwards to Uganda, Kenya, Tanganyika.)

Selected specimens: Khartoum, 1969, Elamin and Elsheikh 1626. Kordofan, Haraza, 1969, Elamin 1603. Darfur, J. Marra, 1969, Elamin 1601. Blue Nile, Singa, 1969, Elamin 1372.

Observation: When the bark is peeled off the branches and then moistened with water, a nasty nitrogenous smell results. This character was also mentioned by Brenan (1959) when dealing with the East-Tropical African specimens of *A. nubica*.

7. A. TORTILIS (Forsk.) Hayne in Getreue Darstellung, 9:31 (1825).

Arabic: Sammar and Seyal.

Type: Yemen, Haes-Jobla, 1775, Forskal (C. holo).

Small shrub to a tree, 1-21 m high. Crown flat, spreading or irregular; one main stem in tree forms and two to many stems in shrubby forms. Bark grey, greyish brown to yellow, smooth or fissured. Young branchlets, yellow, brown, purplish-red, glabrous to pubescent. Stipules spinescent. Spines hooked, dark brown or straight, white; the two types of spines might occur in the same plant; the short hooked or curved spines 2-6 mm long, the straight, white spines 1-10 cm long. Leaves 0.5-3 cm long. Petiole glandular or eglandular, pubescent, 0.2-3 mm long. Rachis glabrous to densely pubescent, grooved adaxially. Pinnae 2-5 paired, 0.2-18 mm long. Leaflets 12-16 paired, 0.5-5 x 0.2-6 mm, dark green or pale green, oblong linear, glabrous to pubescent, margins ciliolate or only at apex, apex obtuse. Inflorescence globose heads, white; peduncle pubescent, 1-2 cm long, involucel on lower half of peduncle. Flowers bisexual and male in the same inflorescence. Calyx 4-5 lobed, pubescent especially at tips, 1-3 x 0.5 mm. Corolla 5-7 lobed, 2 x 0.3 mm, dark tipped. Anthers free, glandular, 3.5 mm long. Ovary 0.7 mm long; style 2.5-3 mm long; sessile or subsessile. Pods spirally twisted or coiled, glabrous to pubescent to densely puberulous, glandular or eglandular, venation longitudinal, margin constricted, colour varies from light green, yellow, brown to pinkish, flat to non-compressed, 5-15 x 0.2-1 cm. Seeds olive-green to red-brown, smooth, elliptic slightly compressed, 6 x 35 mm; areole marginal, U-shaped; funicle 4-5 mm long, coiled; seeds lie longitudinally in the pod. Flowering December-May; fruiting February-May.

Key to infraspecific variants:

1. Trees 7-21 m high. Crown irregular or round; one main stem from base. Leaflets dark green; margin not ciliolate or if so only at the apex. Pods 6-9 mm wide, glabrous to puberulous hairs not seen through naked eye .... subsp. raddiana

1. Shrubs to small trees, 1-7 m high. Crown flat or spreading; two to many stems from base. Leaflets pale green; margin ciliolate. Pods 2-6 mm wide, pubescent , hairs seen through naked eye

   2. Shrub to small tree, 4-7 m high. Crown flat to spreading; two to three stems from base. Bark fissured or smooth, grey. Spines a mixture of long, straight, white spines and short, curved, brown spines. Pods not compressed, 3-6 mm wide, glandular or eglandular .... subsp. spirocarpa

   2. Small shrub, 1-4 m high. Crown flat; many stems from base. Bark smooth, yellow to brown-grey. Spines short, brown, curved; long white spines usually absent, or, if present, slightly curved. Pods compressed, 2-3 mm wide, eglandular .... subsp. tortilis

Subsp. raddiana (Savi) Brenan in Kew Bull. 1957:87 (1957).

Arabic: Seyal.

Syn: A. raddiana Savi, Alc. Acazie Egiz: 1 (1830); Andrews, Fl. Pl. Sudan 2:140 (1952).

A. tortilis sensu Crowfoot, Fl. Pl. N. & C. Sudan 80 (1928) non (Forsk) Hayne.

A. spirocarpa sensu Broun & Massey, Fl. Sudan 169 (1929) [Hochst. ex] A. Rich.

Habitat: Along rivers and seasonal valleys on loamy or gravelly soils on savanna grasslands.

Distribution: Central, Northern and South-East Sudan. (Also in North East and West Africa.)

Selected specimens: Kordofan, Um Garfa, 1969, Elamin 1606. Khartoum, Kilo 10, 1933, Aylmer 84. White Nile, El Ghogalab, 1969, Elsheikh 1401. Kassala, Gedaref, 1931, Cooke 48.

subsp. spirocarpa ([Hochst. ex] A. Rich.) Brenan in Kew Bull. 1957:88 (1957).

Arabic: Sammar.

Syn: A. spirocarpa [Hochst. ex] A. Rich., Tent., Fl. Abyss. 1:239 (1847).

A. spirocarpa [Hochst. ex] A. Rich. var. major Schweinf. in Linnaea, 35:323 (1867-8).

[A. tortilis sensu Broun & Massey, Fl. Pl. Sudan 169 (1929), Andrews Fl. Pl. Sudan, 2:142 (1952) non (Forsk.) Hayne, sensu stricto]

Habitat: Along seasonal rivers and valleys in gravelly soils in dry grass savanna and semi-desert scrub.

Distribution: North, Central and South-East Sudan (East and Central Africa).

Selected specimens: Khartoum, Omdurman, 1970, Elamin 693; Wadi Siedna, 1970, Elsheikh 1488. Kassala, Red Sea Hills, 1932, Aylmer 633. Kordofan, Jebel El Dair, 1962, Wickens 740. Equatoria, Toreit, 1961, Jackson 4246.

subsp. tortilis; Brenan in Kew Bull. 1956:86 (1956).

Arabic: Sammar.

Type: Sudan, Kassala, Suakin, 1869, Schweinfurth 1966.

Syn: Mimosa tortilis Forsk., Fl. Aegypt-Arab. 176 (1775).

A. spirocarpa Hochst. ex A. Rich. var. minor Schweinf. in Linnaea 35:323 (1867-8).

A. spirocarpa sensu Crowfoot, Fl. Pl. N. & C. Sudan 74 (1928) non Hochst. ex A. Rich.

Habitat: Typical desert and semi-desert species, near rivers and valleys on sandy loamy soils.

Distribution: Central and Northern Sudan on desert and semi-desert plains. (Also in North Africa, Ethiopia and Somalia.)

Selected specimens: Kassala, Red Sea Hills, 1966, Kassas E292. Northern Province, Nubia, 1885, Johnson 3. Khartoum, Khor Shambat, 1933, Aylmer 308. Kordofan, Jebel Dair, 1963, Wickens 841.

Observations: With the Sudan specimens of A. tortilis, I could not apply successfully Brenan's synopsis of the subspecies, because the separating characters overlap. Brenan based his synopsis on the indumentum of branches, leaves and pods, pod width, and presence or absence of red glands on the pods. All the Sudan specimens are pubescent in different degrees. The red glands are not constantly present in one subspecies, but are found in subsp. raddiana and absent sometimes in subsp. spirocarpa. The pod width is found to be highest in raddiana, intermediate in spirocarpa and lowest in tortilis, which agrees with Brenan's idea but not necessarily his dimensions.

Schweinfurth, in Linnaea 35:323 (1967-8), made a study of the tortilis group after seeing them in the field, and gave the name A. tortilis Hayne (=A. raddiana Savi) to the subsp. which Brenan called subsp. raddiana. The two subsp. spirocarpa and tortilis of Brenan were grouped by Schweinfurth under the one species, A. spirocarpa, and he initiated two varieties, var. major

(= tree 20'-50' high) and var. <u>minor</u> (= shrub 1'-20' high).

A similar treatment of <u>A. tortilis</u> variants was made by Crowfoot in Flowering Plants of Northern and Central Sudan (1928) after studying the plants in the field. She drew three figures of the three variants, as a tree with one stem (= subsp. <u>raddiana</u>) and a small shrub with many stems and a flat crown (= subsp. <u>tortilis</u>), and a third variant intermediate in form between the other two, with three stems and an irregular crown (= subsp. <u>spirocarpa</u>). She used the names already given by Schweinfurth. After studying this group in the field, I provisionally agree with the results of Crowfoot, but while keeping Brenan's nomenclature, I have added other additional characters concerning habit, crown and bark in my synopsis, which will make the separation of the three subspecies easier in the Sudan. Further study in the Sudan might show that subsp. <u>raddiana</u> would be better reinstated as a separate species from <u>A. tortilis</u>.

8. A. DREPANOLOBIUM /Harms. ex/ Sjostedt, Schwed. Zool. Exped. Kilimanjaro, 8:116-117, t. 6, fig. 7-8, t. 7, fig. 2-3 (1908).

Arabic: Soffar Aswad.

Type: Tanganyika, Kilimanjaro, between Kwagogo and Moshi, Engler 1688 (B, holo, K, drawing).

Shrub or small tree, 2-7.5 m high. Crown spreading or irregular. Bark brown to dark brown with horizontal fissures. Young branchlets pubescent to glabrous. No powdering bark on branches, yellow flakes exposing brown bark. Stipules spinescent. Spines inflated into globose swellings at the base (ant galls, with occasional normal straight spines). Inflated spines grey-white with dark purplish-brown colour with white spots or dark brown swelling with a yellowish-brown band, but always with white spots. Spines 3-4 cm long, glabrous. Leaves: rachis up to 10 cm long, glandular before first pinnae and at the end 2-pinnae, pubescent and grooved adaxially. Petiole 2-3 mm long, glandular. Pinnae 3-13 paired. Leaflets 4 x 0.5-0.7 mm, 15-26 paired, glabrous or minutely ciliolate at margins, apex acute, sub-acute or obtuse. Inflorescent globose, white to cream, peduncle glabrous or slightly pubescent, 1-5.5 cm long; involucel on lower half of peduncle; flower bracts broad, hairy and deflexed inwards. Calyx brown, hairy at tip, 5-6 lobes, 1-5 x 0.5 mm. Corolla yellow to slightly brown, 5-7 lobes, glabrous, 3.5 x 0.5 mm; stamens white, 5.5 mm long. Ovary brown, 0.5-0.7 mm long; style 4 mm; stipe 0.2 mm long. Pods falcate, brown to pinkish, glabrous, dehiscent, 4-6 cm long, 5 -10 mm wide; apex attenuate or accuminate, margin constricted, venation longitudinal. Seeds elliptic, grey to pale brown, compressed, lying longitudinally in the pod, 11 x 4 mm; areole U-shaped, marginal, 6 x 2.5 mm, usually 5-6 seeds per pod; funicle slender, 5 mm long.

Flowering August-December; fruiting February-March.

Habitat: Gregarious on dark grey clays on water depressions in dry grass savanna.

Distribution: In the southern parts of Central Sudan. (Also found in Kenya, Tanganyika, Uganda, Congo, Ethiopia and Somalia.)

Selected specimens: Khartoum (South Blue Nile origin), 1969, Elamin 1659. Kassala, Red Sea Hills, 1966, Kassas E534; Gedaref, 1931, Cooke 72; Gedaref, 1931, Cooke 27.

Observation: This species differs from *A. seyal* var. *fistula* in the colour and length of the inflated spine (ant gall), and in its bark being neither powdery nor whitish green.

9. A. GERRARDII Benth. var. GERRARDII; Brenan in Kew Bull. 1957:369 (1958).

Arabic: Salgam

Type: Natal, Gerrard 1702 (K, holo!).

Syn: A. hebacladoides Harms in Bot. Jahrb. 36:208 (1905); Andrews, Fl. Pl. Sudan 2:144 (1952).

Tree 5-15 m high. Crown irregular. Bark black, deeply fissured. Branchlets densely pubescent, epidermis on branches peels off to expose a rusty-brown bark. Stipules spinescent. Spines straight, 1-7 cm long, grey or rusty-red, sometimes with a gall-like swelling at the base, pubescent. Leaves 5-10 cm long. Petiole 0.5-1 cm, glandular, pubescent. Rachis 5-9 cm long, glandular, pubescent, grooved adaxially. Pinnae 4-15 paired, 1-4 cm long. Leaflets 12-30 paired, linear oblong, dark green adaxially and pale on the abaxial surface, 1.5-4 mm x 0.5-1 mm, midrib visible on both surfaces, margin ciliolate, apex subacute or obtuse. Inflorescence in globose heads, creamy white; peduncle pubescent, 1.5-3.5 cm long; involucel on the lower half of the peduncle; floral bract brown, non-stalked and pubescent. Calyx white, pubescent, 1.5 x 0.3 mm. Corolla white with green tips, glabrous, 3 x 0.5 mm. Stamens free, glandular, 6.5 mm long. Ovary brown, 10 mm long; style 7 mm long; stipe 1 mm long. Pod falcate, margin constricted to entire, pubescent, dark brown to rusty-red, dehiscent, 6-15 x 0.4-1 cm, venation longitudinal. Seeds 5-8 in the pod, grey-brown, oblong, compressed, smooth, 9 x 4.5 mm, lying on a yellow-white band on ventral surface of pod; areole U-shaped, marginal, 7.5 x 3 mm; funicle long and slender, 7.5 mm long.

Habitat: Gregarious on alkaline grey day in the deciduous savanna woodlands, usually above 600 mm of rainfall.

Distribution: Central and Southern Sudan. (Widely spread in Tropical

Africa, southwards to Natal and westwards to Nigeria.)

Selected specimens: Khartoum Botanic Garden (origin Nuba Mts.) 1969, Elamin 1415. Darfur, Radom, 1969, Elamin 1502; Adda, 1969, Elamin 1594; Nyala, 1969, -- 117.

Observation: This species is very distinct in the field by the dark blackish fissured bark.

10. A. PAOLII Chiov. in Ann. Bot. Roma, 13:395 (1915).

Type: Ethiopia, Ogaden, between Berdera and Mansur, Paoli 578, and Heima, Paoli 611 (K, photos!).

Small shrub, 1.5-2.4 m high. Crown obconical, branching from base. Bark dark green to grey-green, smooth. Branchlets light brown, densely pubescent, with white bristles, 3-4 mm long, which cover all vegetative parts of the plant. Stipules spinescent, straight, white to light brown, hairy, 5 cm long. Leaf 5 cm long. Rachis pubescent, grooved adaxially. Pinnae 4-9 paired, 2-5 cm long. Leaflets 7-15 paired, 6 x 2 mm, margin with appressed cilia, apex round to subacute; midrib visible on both surfaces. Inflorescence in globose heads; peduncle pubescent, 1.8 cm long; involucel on lower half of peduncle. Flower creamy white, sessile. Calyx pubescent, 2 x 1 mm. Corolla pubescent, 3 x 1 mm. Stamens white, free, glandular, 5.5 mm long; anthers red. Ovary 1.5 mm long; style 5 mm long; stipe 1 mm long. Pods straight or nearly falcate, coriaceous, dehiscent, covered with dense bristles, 3-4 mm long, apex attentuate, 10 x 0.8 cm; venation longitudinal. Seeds olive-brown, slightly wrinkled, not or sparsely compressed, 6-8 x 5 mm; areole U-shaped, marginal, 5-6 x 3-3.5 mm; funicle 4 mm long.

Habitat: On alluvial or colluvial soils on dry grasslands.

Distribution: Dry grasslands scrub of South-East Equatoria. (Also found in Ethiopia, Somaliland and Kenya.)

Specimens seen: Equatoria, Moro-Yakipi, 1941, Myers 13999. Jackson (1966) collected some specimens from Kapoeta, but these have not been seen by me.

Observation: This species is closely related to A. nubica but quite distinct by the indumentum and pod characters. The indumentum is seen through the naked eye covering all vegetative parts of the plant.

11. A. MACROTHYRSA Harms, in Bot. Jahrb. 28:39 (1900).

Type: Tanganyika, Iringa, Goetze 653 (B, holo, K, iso!).

Tree 13-16 m high. Bark dark grey-brown, with rough fissures. Branchlet yellow, glabrous to pubescent. Stipules spinescent. Spines straight, stout, flattened adaxially, brown to grey, pubescent, 1.8 cm long. Leaves largest amongst the Acacias, 30-60 cm long. Petiole pubescent, glandular, 0.2-3 cm long. Rachis 30-57 cm long, grooved adaxially, pubescent, glandular before the last 2-3 pinnae. Pinnae 17-18 paired, 15 cm long. Leaflets 50-60 paired, margin ciliolate, apex acute to subacute, 7-8 x 1-1.5 mm. Inflorescence in globose heads, paniculate, orange, large, 1.5 cm diam.; peduncle pubescent, 3.5-4 cm long; involucel on lower half of peduncle; floral bract spoon-shaped, pubescent and dark. Calyx 4-6 lobed, orange, pubescent, 1 x 0.5 m, about quarter length of petals. Corolla 5-lobed, orange, glabrous, 4 x 0.6 mm. Anthers free, glandular, orange, 6 mm long. Ovary brown, 1.5 mm long; style 5 mm long; stipe 0.1 mm long. Pods orange to orange-red or brownish red, flattened, straight or slightly falcate, glabrous, dehiscent, coriaceous, apex rostate, 16 x 2 cm. Seeds 8 to the pod, light brown, glabrous, orbicular, 6.5 x 6 mm; areole central crescent-shaped, 1.5 x 2 mm; funicle red-brown, 8 mm long; seeds lie horizontally in pods. Flowering October-December; fruiting January.

Habitat: Tropical woodlands on red iron-stone soils; sometimes on rocky hillsides. Rainfall is above 1200 mm.

Distribution: Equatoria and Bahr Elghazal provinces. (Tropical parts of Africa, like Ghana, Nigeria, Congo, Portuguese East Africa, Nyasaland and South and North Rhodesia.)

Selected specimens: Khartoum Bot. Garden (origin Bahr Elghazal province) 1970, Elamin 1630. Equatoria, Mangalla, 1936, Sandeson 41; Lado, 1915, Wood 2; Kagalo, 1931, Turner 77; Loka, 1929, Simpson 7343; Amadi, 1937, Myers 6912.

Observation: This species is very distinct amongst the Acacias by the enormous size of its leaves which can reach up to 60 cm long. Its inflorescence is paniculate with striking orange flowers. The spines which are grey to brown may look like falcate prickles, but they are spinescent stipules which are flattened adaxially.

12. A. SEYAL Del., Fl. Egypt, 142, t. 52, fig. 2 (1813).

Arabic: Talh and Saffar Abiad.

Type: Egypt, Delile (MPU, holo).

Tree 3-17 m high. Crown spreading or irregular. Bark powdery, smooth or sparsely flaking, whitish to greenish yellow or orange-red, sometimes green and red bark occurs in the same tree. Young branchlets almost glabrous, with numerous reddish glands, epidermis of branches becoming reddish and flaking to expose greenish or reddish powdery bark. Stipules spinescent. Spines 10 cm long, inflated (ant galls) in var. fistula and absent in var. seyal, other prickles absent. Leaves 1-12 cm long; glands on petiole and before last 1-2 pinnae; rachis 7 cm long. Pinnae 3-9 paired. Leaflets 7-20 paired, 3-7 x 0.5-1.3 mm, oblong to linear, apex obtuse to subacute, base oblique, glabrous surface but ciliolate margins. Inflorescence capitate, yellow; peduncle 1-4 cm long, glabrous; involucel on lower half of peduncle; flower bracts pubescent, medium line conspicuous, 2.5 mm long. Calyx pubescent, 4-6 lobed, white to yellow, apex reflexed backward, 2 x 0.5 mm. Corolla 5-6 lobed, glabrous, darker than calyx, 4.5 x 0.8 mm. Anthers glandular, yellow, free, 9 mm long. Ovary sessile, brown, 0.5 mm long; style 3-4 mm long. Pods falcate, dehiscent, constricted between seeds, glabrous, venation longitudinal, red gland on pod surface conspicuous, 7-22 cm long, 0.5-0.9 cm wide. Seeds olive to olive-brown, glabrous, wrinkled, compressed, elliptic, lying longitudinally in the pod on a white thin band which runs longitudinally in the pod, 7 x 3-4.5 mm; areole marginal, U-shaped, 4 x 2 mm; funicle very long and coiled, 1.5 cm long. Flowering November-April; fruiting January-May.

Habitat: Dark cracking clay. Found often on higher slopes of the rivers and valleys in addition to the hard clay plains of Central Sudan. Also in clay depression areas where water is accumulating part of the year.

Distribution: Widely spread all over the Sudan. (Elsewhere in Northern Tropical Africa to Egypt. Var. fistula is found in East Africa, Portuguese East Africa, Nyasaland and Rhodesia.)

Infraspecific variants:

There are two varieties in the Sudan, separated as follows :

Inflated spines (ant galls) absent; bark green-whitish and red .... var. seyal

Inflated spines (ant galls) present; bark green-whitish only .... var. fistula

var. seyal Brenan in Fl. Trop. East Africa, 103 (1959).

Arabic: Talh.

Type: Egypt, Delile (MPU, holo).

Syn: A. seyal auct. plur.

Habitat: Savanna grassland or woodland or dry cracking clay.

Distribution: All over the Sudan, especially central parts. (Also in East and North Africa, extending to Egypt).

Selected specimens: Khartoum, Soba, 1969, Elamin 1440. Blue Nile, Singa, 1969, Elamin 459. Kordofan, El Obeid, 1969, Elamin 1421. Darfur, J. Marra, 1969, Elamin 1547. Darfur, Ragag, 1969, Elamin 1568. Kassala, Hawata, 1969, Elamin 1654.

var. fistula (Schweinf.) Oliv. in Fl. Trop. Afr. 2:351 (1871).

Arabic: Soffar Abiad.

Type: Sudan, Gedaref, 1965, Schweinfurth (MPU, holo).

Syn: A fistula Schweinf. in Linnaea 35:344 (1867-8).

Habitat: Deciduous forests on clay depression areas where water accumulates part of the year.

Distribution: Central and South-East Sudan, especially east of the Nile. (Also in East Africa, Nyasaland and Northern Rhodesia.)

Selected specimens: Kassala, Red Sea Hills, 1966, Kassas E548; Hawata, 1970, Elamin 6543. Blue Nile, Tozi, 1966, Kamali 755; Singa, 1969, Elamin 2977. Upper Nile, Pipor River, 1929, Simpson 7068. Equatoria, Huba, 1929, Simpson 7298; Equatoria, White Nile, 1913, Lynes s.n.

Observation: A. seyal var. seyal has a red or green bark or a mixture of red and green in the same plant, but var. fistula always has green-whitish smooth bark only. It is noticeable that in west of the Nile there are very few var. fistula and this might explain its absence from West Africa. The only two inflated spine (ant galls) Acacias, namely var. fistula and A. drepanolobium, occur almost in the same area in Central Sudan, East of the Nile. They are easily separable by the bark, which is green and smooth in var. fistula and rough fissured brown in A. drepanolobium, also the inflated spines are dark purplish-brown to black and are only 3-4 cm long (Arabic: Soffar Aswad - black Whistler), and those of var. fistula (Arabic: Soffar Abiad - white Whistler) are white and up to 10 cm long. The term "ant gall" can be misleading as the swelling is not a gall and it is not only ants but other insects that make a pore and infest the inflated swelling. Also many of these swellings are never infested by insects at all. The Arabic names given to these two plants mean "black Whistler" because of the whistling sound made by the wind against the insect pores on the black inflated spines of A. drepanolobium, and "white Whistler" for the white inflated spines of var. fistula.

A. seyal var. fistula usually exists in pure stands or mixed with var. seyal, and here var. seyal will have green-whitish bark like var. fistula.

13. A. HOCKII De Wild. in Fedde Repert, 11:502 (1913).

Type: Belgian Congo, Katanga, Luafu Valley, Hock (BR, holo).

Syn: A. stenocarpa sensu Broun & Massey, Fl. Sudan 171 (1929), non Hochst.

A. seyal Del. var. multijuga [Schweinf. ex] Bak. f. Legum. Trop. Africa :844 (1930).

Trees 5-12 m high. Bark red or yellowish brown, not powdery. Young branchlets densely pubescent with numerous red glands and red-brown bark which does not peel to expose a powdery bark. Stipules spinescent. Spines straight, not inflated, white, brown or grey, short, 1-1.5 cm long, sometimes hairy. Leaf 1-7 cm long, petiole glandular, 0.5-1 cm long. Rachis 2-6 cm long, pubescent, glandular at end 2-3 pinnae. Pinnae 3-9 paired. Leaflets 10-20 paired, 2-6.5 x 1-1.3 mm, margins ciliolate, apex acute. Inflorescence in globose heads; peduncle pubescent, 5-12 mm long; involucel on upper half of the peduncle; floral bracts glandular, 1-3 mm long. Flower yellow, sessile. Calyx pubescent, glandular at tips, 1.2 x 0.3 mm. Corolla glabrous, darker than calyx, 2.3 x 0.5 mm. Stamens, yellow, free, glandular, 3 mm long. Ovary 0.8 mm long; style 2.5 mm long; stype 0.2 mm long. Pods dark pinkish or yellow-greyish with red glands (other characters of pod like A. seyal). Seeds dark olive, elliptic; areole marginal, U-shaped; funicle 4 mm long.

Habitat: Deciduous woodland on loamy soils and on hilly ground.

Distribution: Red Sea Hills, Central and Southern Sudan. (Widely spread in Tropical East, Central and West Africa.)

Selected specimens: Kassala, Red Sea Hills, 1966, Kassas & Obeid E677. Bahr Elghazal, Wau, 1969, Elamin 677. Equatoria, Katire, 1970, Silvio 4; Bongoland, 1869, Schweinfurth 2627; Loka, 1937, Myers 6906; Yei, 1931, Turner 69.

<u>Observation</u>: <u>A. hockii</u> is related to <u>A. seyal</u> but differs in the bark not being powdery and in its glandular branches and pods; its flowers are small in size compared with <u>A. seyal</u>. The spines in <u>A. hockii</u> are slender, shorter and hardly reach 4 cm, and are never inflated, and its involucel is on the upper half of the peduncle, while in <u>A. seyal</u> it is on the lower half of the peduncle.

14. A. EHRENBERGIANA Hayne in Getreue Darstellung. 9:29 ex tab 29 (1825).

Arabic: Sallam.

Type: Sudan, Nubia, Ehrenberg (1825).

Syn: A. flava Schweinf. in Bull. Herb. Boiss. 4:214 (1896).

Shrub 1-5 m high. Crown irregular. Bark of young branches and stem peeling into yellow flakes exposing pinkish bark; bark of old stems grey, rough and fissured. Many stems arise from the base. Young branchlets pinkish-brown, pubescent. Stipules spinescent. Spines straight, white, pubescent, usually longer than the leaf, up to 8 cm long, together with shorter spines. Leaves small, up to 2 cm long. Petiole short, 0.5 cm, hairy, eglandular. Rachis pubescent, striate, grooved adaxially, 1.5 cm long, glandular before last 2-3 pinnae. Pinnae 1-1.5 cm long, 1-3 paired. Leaflets 10-12 paired, oblong-linear, 4.5 x 0.5 mm, margin ciliolate, apex obtuse, midrib visible abaxially. Inflorescence capitate, yellow; peduncle pubescent, 2.5 cm long; involucel on lower half of peduncle; floral bract hairy, brown, 1.7 mm long, with a visible medium line on its stalk. Flowers yellow, sessile. Calyx pubescent, tip green, reflexed inwards, 1.5 x 0.3 mm. Corolla pubescent, tip green, reflexed backwards, 2.5 x 0.8 mm. Anthers free, 5 mm long. Ovary brown, 1.7 mm long; style 4 mm; stipe 0.2 mm long. Pods falcate, pink or brown or grey or olive-green, constricted, glabrous (same as seyal); venation longitudinal. Seeds brown, smooth elliptic, 7-10 seeds in the pod, 5 x 3 mm; areole marginal, U-shaped, 4 x 2 mm; funicle 4.5 mm long. Like seyal it has a yellow band of thin sheet under the seeds. Flowering December-May; fruiting February-May.

Habitat: Dry sandy plains with rainfall less than 100 mm.

Distribution: Northern desert and semi-desert parts. In Africa it is found in countries north of the Sahara.

Selected specimens: Northern Province, Jebel Awinat 1932, Shaw 3; Delau Well 1933, Cooke 149. Khartoum, Wadi Siedna, 1970, Elamin & Elsheikh 1625; Soba, 1970, Elamin 2215. Blue Nile, Medani-Khartoum Road, 1930, Aylmer 82. Kassala Red Sea Hills, 1933, Cooke 116; Suakin-Berber, 1868, Schweinfurth 666.

Observation: *A. ehrenbergiana* is related to *A. seyal* but distinct in its arid sandy habitat, non-powdered bark, branching from base, and its pinnae pairs never exceeding 3. Its spines are pubescent and always longer than leaves.

15. <u>A. NILOTICA</u> (L.) [Willd. ex] Del., Fl. Egypt 3:79 (1813).

Arabic: Sunt, Garad.

Type: Egypt, Herb. Linnaeus 1228.28 (Linn.Syn).

Syn: <u>Mimosa nilotica</u> L., Sp. pl. :521 (1753).

<u>Mimosa scorpioides</u> L., Sp. pl. :521 (1753).

<u>Mimosa arabica</u> Lam. Encycl. 1:19 (1783).

<u>Acacia arabica</u> (Lam.) Willd., Sp. pl. 4:1084 (1806); Crowfoot, Fl. Pl. N. & C. Sudan 77 (1928); Broun & Massey, Fl. Sudan 169 (1929); Andrews, Fl. Pl. Sudan 2:147 (1952).

Tree 5-25 m high. Bark dark grey, brown or black, rough and fissured. Young branchlets brown, grey or pink, glabrous to pubescent. Stipules spinescent. Spines straight, white, pubescent, 1-8 cm long. Leaves 2-7 cm long. Petiole glandular, 1.3 cm long. Rachis tomentose, up to 6 cm long, glandular at end 1-3 pinnae, grooved adaxially. Pinnae 4-9 paired, 2.5-3 cm long. Leaflets 7-30 paired, glabrous to pubescent, 1.5-6 x 0.5 mm, margin ciliolate, apex acute to mucronate. Inflorescence in globose heads, yellow; peduncle pubescent, 1.5-3 cm long; involucel on upper part of peduncle, subtending 1-3 flowers, floral bracts pubescent, 1.5 x 0.3 mm. Flowers sessile, yellow, bisexual, and male flowers in the same inflorescence. Calyx 4-6 lobed, pubescent, darker than petals, 1.5 x 0.6 mm. Corolla 4-6 lobed, pubescent, yellow, 2.5 x 0.8 mm. Anthers free, glandular, 5.5-6 mm long. Ovary brown, glabrous, 0.9 mm long; style 5.5-6 mm long; stipe 0.2 mm long. Pods variable, necklaced or not, margins crenate or nearly entire, dehiscent, straight or slightly falcate, glabrous to pubescent, dark brown to dark grey, 5-20 x 1-2 cm; surface ridged, venation longitudinal or not apparent, 10-12 seeds to the pod. Seeds dark brown or brownish-black, elliptic to subcircular, 8 x 6 mm; areole marginal, U-shaped or closed O-shaped; funicle thin, brown, 3 mm long; seeds lie longitudinally, obliquely or horizontally inside pods. Flowering July-September; fruiting March-May.

Key to infraspecific variants:

1. Pods necklace-like; margin narrowly and regularly constricted between seeds
   2. Pods glabrous .... subsp. nilotica
   2. Pods tomentose .... subsp. tomentosa
1. Pods not necklace-like; margins straight or crenate
   3. Pods margin crenate, West and Central Sudan .... subsp. astringens
   3. Pods margin straight or nearly so, Equatoria, South-East Sudan .... subsp. subalata

subsp. nilotica; Brenan in Kew Bull. 1957:84 (1957).

Syn: A. nilotica (L.) Del. var. typica Hill in Bot. Mus. Leafl. Harvard Univ. 8:98 (1940).

A. nilotica (L.) Del. var. nilotica Cufodontis in Bull. Jard. Brux. 25:195 (1955).

A. nilotica sensu Andrews, Fl. Pl. Sudan 2:147 (1952) [Willd. ex] Del.

Habitat: Riverine species along banks of the Nile and its tributaries, on light silty soils.

Distribution: North, South and Central Sudan (widely distributed in Africa).

Selected specimens: Blue Nile, Singa, 1969, Elamin 3034. Khartoum, Green Belt, 1970, Elamin 30. Northern Province, Berber, 1868, Schweinfurth

609. Blue Nile, Dinem, 1929, Chipp 1.

subsp. tomentosa (Benth.) Brenan in Kew Bull. 84 (1957).

Syn: A. arabica (Lam.) Willd. var. tomentosa Benth. in Hook., Lond. Journ. Bot. 1,500 (1842).

Habitat: Along banks of the Nile and its tributaries, on light silty soil.

Distribution: As subsp. nilotica in North, South and Central Sudan, often mixed with it or pure stands in Northern Province. (In Africa as subsp. nilotica.)

Selected specimens: Khartoum, Soba, 1970, Elamin 1397. Northern Province, W. Nile, 1869, Schweinfurth 928. Kassala, Gash Delta, 1967, Sahni & Kamil, 618. Upper Nile, Shullok Country, 1863, Speke & Grant 769.

subsp. astringens Roberty in Candollea 11:150 (1948).

Syn: A. nilotica (L.) Del. subsp. adansonii Brenan in Kew Bull. 1957:84 (1957).

Habitat: Along banks of seasonal rivers and valleys on alluvial light soils.

Distribution: Restricted in Kordofan, Darfur and Northern Bahr Elghazal. (Elsewhere in West Africa.)

Selected specimens: Khartoum, 1970, Elamin 1660; Green Belt, 1970, Elsheikh 1668. Blue Nile, Medani, 1969, Elamin 3001. Kordofan, Elobeid, 1969, Elamin 1420. Darfur, Nyala, 1969, Elamin 1504. Bahr Elghazal, Wau, Latif 2017.

subsp. subalata (Vatke) Brenan in Kew Bull. 1957:85 (1957).

Syn: A. subalata Valke in Oesterr. Bot. Zeitschr. 30:276 (1880).

Habitat: Woody grassland on gravelly soil forming thorn thicket with _Commiphera Africana_.

Distribution: Restricted to the South-East Equatoria Province. (Also in Kenya, Tanganyika and Uganda.)

Selected specimens: Equatoria, Katire-Toriet Road, 1961, _Jackson_ 4229; Kadefoo River, 1950, _Myers_ 13451; Mangalla, _Grabham_ G13.

Observations: subspp. _nilotica_ and _tomentosa_ are associated together in habitat in permanent watercourses along the Nile, and can withstand water inundation for three months or more. They extend southwards to Upper Nile and occasionally in Equatoria, but they are usually replaced by _A. sieberana_ in their southern sites. The other two subspecies _astringens_ and _subalata_ are related in their pod shape, which is not necklaced, and separated by the straight or almost entire margin of pods in _subalata_, together with its habitat and distribution in South-East Equatoria. Subsp. _astringens_ is almost limited to western parts of Central Sudan on seasonal watercourses; its distribution east of the Nile is occasional. It is one of the most variable species of Acacias. Pod specimens collected by A. Houri along the Blue Nile show extraordinary elongations of the constrictions between the seeds, but they are necklace-shaped and tomentose, and I put them under subsp. _tomentosa_. Brenan recognises three other subspecies not existing in the Sudan. The species exists widely in Africa, Asia and Central America, a probable reason for its extreme variation.

16. A. KIRKII Oliv. subsp. MILDBRAEDII (Harms.) Brenan in Kew Bull. 1957:364 (1958).

Type: Belgian Congo, Kwenda, Mildbraed 1887 (B. Syn).

Syn: A. mildbraedii Harms, Wessen. Eng. (1907-1908); Andrews, Fl. Pl. Sudan 2:147 (1952).

Tree up to 18 m high, flat crowned. Bark pale green, smooth, peeling or scaling. Branchlets pubescent. Stipules spinescent. Spines grey-brown or white, with dark tips, straight, glabrous, up to 8 cm long. Leaves 3 cm long, grooved adaxially. Petiole 0.3 cm long. Pinnae 5-14 paired. Leaflets 10-25 paired, linear oblong, dark green, 2.5 x 0.5 mm, apex acute to mucronate, surface of leaf granulate, margin sparsely ciliolate. Inflorescence in globose heads; peduncle pubescent and glandular, 2 cm long; involucel on lower half of peduncle. Flowers red, sessile. Calyx 2 x 0.5 mm, yellow. Corolla red, 4 x 0.5 mm. Stamens white, glandular, free, 4 mm long. Ovary 1 mm long; style 4 mm long; stipe 1 mm long. Pods pale-brown, 6 x 1 cm, flat, coriaceous, margins constricted like a necklace, glabrous, venation radiating to the centre of the segments; joints of pods are without any central projections. Seeds olive-brown, smooth, subcircular to elliptic, compressed, 5-7 x 4.5 mm; areole U-shaped, marginal, 4 x 3 mm; funicle 3 mm long.

Habitat: In swamps or on margins of lakes and rivers on light, silty soils.

Distribution: Equatoria Province. (Also in Tanganyika, Uganda, Congo and Ruanda-Urundi.

Specimen cited: Equatoria, Juba, 1926, Aylmer GA27/15.

Observation: This is very closely related to A. nilotica in its habitat and the necklace pods, but differs in its flat crown and the flattened pods with the radiating venation towards the centre of the pod segments. In A. nilotica the segments are smooth or with raised ridges, but venation is not apparent, and also the pods are not flattened, with a dark grey to blackish colour.

This subsp. mildbraedii differs from the other subsp. kirkii in that the latter has the joints of the pods with a medium or small wart-like projection up to 4-5 mm high in the centre of each of their flat sides. In subsp. mildbraedii the joints of the pods are without any central projections.

17. A. DOLICHOCEPHALA Harms, in Ann. 1st Bot. Roma 7:86 (1897).

Type: Ethiopia, between Rogono and Gobo Duaya (Gall Sidamo, 5° 33' N., 38° 8' E.), Riva 599 (Fl. holo).

Small tree 4-7.5 m high. Branches dark brown or grey-brown, glabrous, with circular white lenticels, branches usually arise from a scaly woody stalk at the nodes. Stipules spinescent, straight, slender, white, short, up to 5 mm long. Leaf 4-9 cm long. Petiole 1.5 cm long, glandular. Rachis 5-7.5 cm long, pubescent, grooved adaxially. Pinnae 6-14 paired, 3.5 cm long. Leaflets 12-35 paired, 2.5-7.5 x 0.6-2 mm, glabrous, margin not ciliolate, apex round to subacute, midrib visible on both surfaces. Infloresence ellipsoid or sub-globose (intermediate between spicate and capitate); peduncle very long, 4-7.5 cm long, pubescent; involucel on upper half of peduncle usually subtending 2-3 flowers. Flower sessile, yellow-cream. Calyx glabrous, short 0.8 x 0.2 mm. Corolla glabrous tips reflexed backward, 4 x 0.5 mm. Stamens free, glandular, 6.5 mm long; ovary 1.2 mm long; style 5 mm long; stipe 0.2 mm long. Pods dark to purplish-brown, oblong, straight or slightly falcate, coriaceous, dehiscent, glabrous, flattened, venation, longitudinal or oblique, 5-10 x 1.3-1.9 cm. Seeds elliptic, olive-green, compressed, 5.5-6 x 4-5 mm; areole central, U-shaped, 2.5 x 1-1.25 mm; funicle brown, 5 mm long. Seeds lie horizontally in pod.

Habitat: Riverine woodland and foot of rocky hills in tropical regions.

Distribution: In the Sudan it is found at the foot of Equatoria Mountains, e.g. Didinga and South Sudan at 1200 m altitude. (In Africa it is found in Ethiopia, Uganda and Tanganyika.)

Specimen cited: Equatoria, Didinga Mts., 1939, Myers 11219.

<u>Observation</u>: The only species with sub-globose inflorescences, and thus is intermediate between the spicate and capitate types. The flowers found in the involucel bract is a character also found in <u>A. nilotica</u>, <u>A. seyal</u> and <u>A. hockii</u>.

18. A. HORRIDA (L.) Willd. subsp. BENADIRENSIS (Chiov.) Hillcoat & Brenan in Kew Bull. 1958:40 (1958).

Type: Somalia, Magadiscio, Paolii 94 (Fl, lecto!) 131 bis (Fl, Syn!).

Syn: A. latronum (L.f.) Willd., Sp. Pl. 4:1077 (1806).

A. benadirensis Chiov., Fl. Somala 2:183 (1932).

A. latronum (L.f.) Willd. subsp. benadirensis (Chiov.) Brenan in Kew Bull. 1956:191 (1956).

Shrub 1-3.6 m high, flat crowned, branching from the base. Stem dark brown with yellow horizontal lenticels. Stipules spinescent. Spines straight, white, 2.5 cm long, sometimes inflated into elongated galls (like A. elatior). Leaves 2-5 cm long. Petiole eglandular, pubescent. Rachis eglandular, pubescent. Pinnae 2-4 paired. Leaflets 8-10 paired, 3 x 0.5 mm, glabrous, apex acute to subacute, midrib visible at adaxial surface. Inflorescence cylindrical spikes white with an involucre bract (not seen in other spicate Acacias), 2-4.5 cm long. Flowers sessile, white-creamy. Calyx 0.3-1 mm, pubescent. Corolla 2-2.5 mm long, glabrous. Anthers glandular, stamen 5 mm long. Pods brown, kidney-shaped, or falcate, flat, glabrous to pubescent, dehiscent, venation oblique, 3-6 x 1.2-2.5 cm. Seeds obovate to oblong, lie horizontally in pod, compressed, glabrous, 5 x 4.5 mm; areole central, crescent-shape, 1 x 1.5 mm; funicle brown, 7 mm long.

Habitat: Clay thornland.

Distribution: Equatoria, Kopoeta district. (Also found in Uganda, Kenya, Somalia and Ethiopia.)

Specimens cited: Equatoria, Sudan, Ethiopia borders, 1941, Myers 14087.

Observation: A. horrida was reported by J. K. Jackson (1966) to be present in South-East Equatoria, but I have not seen his specimens.

The shape of the pods is unique amongst the Sudan Acacias, being kidney-shaped. It is also prominent in having spicate inflorescence and belonging to Group I. It is allied to <u>A. lahai</u> found in southern parts of Africa.

19. A. MELLIFERA (Vahl) Benth. subsp. MELLIFERA; Brenan in Kew Bull. 1956:191 (1956).

Arabic: Kitir.

Type: Arabia, Surdud, and elsewhere, Forskal (C, holo).

Syn: Mimosa mellifera Vahl, Symb., 3:103 (1791).

Inga mellifera (Vahl) Willd., Sp. Pl., 4:1006 (1806).

Acacia mellifera (Vahl) Benth. in Hook. Lond. Journ. Bot., 1:507 (1842); Crowfoot, Fl. Pl. N. & C. Sudan, 72 (1928); Broun & Massey, Fl. Sudan, 172 (1929); Andrews, Fl. Pl. Sudan, 2:136 (1952).

Shrub 1-9 m high; crown round, branching from base. Bark smooth, grey to brown; lenticels white, horizontal. Young branches glabrous to pubescent. Stipules not spinescent; prickles in pairs below each node, brown to black, falcate, 2-6 mm long. Leaves 2-3 cm long. Petiole glandular with a dark brown pubescent pulvinus 0.8-2.5 cm long. Rachis glabrous to pubescent, glandular between the top 1-2 pinnae pairs, grooved adaxially, 2-3 cm long. Pinnae 2-paired, with a dark pubescent pulvinus 5-6 mm long. Leaflets 1-paired only, stalked with a 1 mm long stalk, obliquely obovate to obovate elliptic, glabrous or pubescent, apex rounded, emarginate or subacute and often apiculate at apex. Venation is visible on both sides, midrib lateral and not central, 3.5-22 mm x 2.5-16 mm. Inflorescence cylindrical spikes 4-5 cm long. Flowers white-cream, pedicellate 0.75-1.5 mm long. Calyx 0.6-1 mm long glabrous, yellow to pinkish, 5-lobed. Corolla yellow-pinkish or pink, 2.5-3.5 mm long, 5-lobed. Stamens 4-7 mm long, glandular, free or united up to 1 mm length. Ovary glabrous, 1.5 mm long; style 7 mm long; stipe 1 mm long. Pods yellow, straw-colour, oblong, straight, dehiscent, membranous, apex round, acuminate or apiculate at apex, 4.5-8 cm long, 13.3-2.5 cm wide, venation horizontal. Seeds 3-5 in pod and lie horizontally, orbicular or ovate, 6-7 x 5-6 mm; areole central crescent shape, 1.8-2.5 mm; funicle 8.5 mm. Flowering July-September; fruiting January-March.

Habitat: In dry, hard, clay soil plains; found pure or mixed with A. laeta, A. senegal, A. nubica and A. seyal.

Distribution: Clay plains of Central Sudan spreading northwards and southwards to the dry thorn scrub areas. (Found in all parts of Africa. Subsp. detinens is of a southern distribution in Africa found in Tanganyika, Rhodesia, South Africa and South-West Africa; also in Ghana and Nigeria.)

Selected specimens: Khartoum, Soba, 1969, Elamin 1489. Blue Nile, Medani, 1970, Elamin 1987. Blue Nile, Singa, 1970, Elamin 2978. Kordofan, Elobeid, 1970, Elamin 1422. Kassala, N. Kasslatown, Elamin & Elsheikh 1657.

Observation: subsp. detinens Brenan has pinnae 3-4 paired, and sub-globose inflorescence; it is absent from the Sudan and it seems to have a southern distribution in Africa.

The leaflets in A. mellifera are large and obovate in shape. The only other species which has similar shape and size of leaflets is A. laeta; this character separates them from the rest of the Sudan Acacias. The pedicellate flowers are also unique amongst the Sudan Acacias. Subsp. mellifera is found in the Sudan to be associated with members of Group I (the spinescent stipules).

One specimen Elamin 1489 from Soba, near Khartoum, was found to have a globose inflorescence in the same cylindrical spike, a feature which is abnormal but might throw a light on the change from cylindrical to globose inflorescences. The globose inflorescences are thought by many authors to have arisen by a process of condensation of the spicate ones, but the phenomena found in the above-mentioned specimens might indicate that they arise from separate pedicellate flowers which develop the pedicel into a peduncle carrying the globose head.

20. A. LAETA /R. Br. ex/ Benth. in Hook. Journ. Bot. 1:508 (1842).

Arabic: Shubahi.

Type: Ethiopia, without locality, Salt (B.M., holo!).

Shrub 2-6 m high. Crown round. Bark smooth, grey, with horizontal lenticels. Young branches grey to green-brownish, glabrous. Stipules not spinescent. Prickles in pairs just below each node, falcate, tip dark brownish to purplish, base grey-whitish, sometimes with dark spots, glabrous, 3-6 mm long. Leaves 3-5 cm long. Petiole pubescent, glandular. Rachis glabrous to pubescent with glands between the top pair of pinnae. Pinnae 2-3 paired. Leaflets 3-5 paired, 4-20 mm long, 2-10 mm wide, obliquely obovate, elliptic or oblong, glabrous to pubescent, margin white and ciliolate, apex acute to apiculate, venation visible on both sides, midrib central. Inflorescence cylindrical, spikes 5-8 cm.long, on 0.5-2 cm pubescent or glabrous peduncles. Flowers white-cream, pedicellate, dark brown, pedicel 0.5-1 mm long; calyx 1.5 x 1 mm, glabrous to pubescent at tip, slightly pinkish; corolla glabrous, pinkish, 4 x 1 mm. Stamens shortly connate at base to 1 mm and 7-8 mm long. Ovary 2 mm long; style 9 mm long; stipe 0.1 mm long. Pods yellow or straw-colour, membranous, flat, straight, oblong, glabrous, apex round to acuminate or apiculate, venation horizontal, 3-5-8.5 x 1.5-2 cm. Seeds 3-5 in pod, orbicular or obovate, flat, light brown, 7 x 5.5 mm; areole central crescent-shaped, 1-8 x 2.4 mm; funicle 7-8.5 mm long. Flowering November-January; fruiting January-March.

Habitat: Associated with Acacia mellifera scrub on clay plain or loamy soils.

Distribution : Central clay plains of the Sudan. Found in North and

North-East Africa, in the west to Nigeria, Ivory Coast and Nigeria and Kenya and Tanganyika.

Selected specimens: Northern Province, Nubia, 1820-26, Ehrenberg 2101. Kassala, Roker, 1949, Bally 6974; J. Elba, 1933, Cooke 139; Suakin, 1864, Schweinfurth 1931. Khartoum, Soba, 1970, Elsheikh 1437. Kordofan, Elobeid, 1970, Elamin 1418; 1961, Jackson 4368; 1969, Wickens 3079. Bahr Elghazal, Niamlelle, 1969, Elamin 4901.

21. A. HECATOPHYLLA [Steud. ex] A. Rich. Tent. Fl. Abyss. 1:242 (1847).

Type: Ethiopia, Schimper, (K, isosyn!)

Small tree 4.5-7.5 m high. Bark grey-white, longitudinally fissured. Young branches tomentose. Young branchlets pubescent or glabrous, lenticellate. Stipules not spinescent. Prickles few or absent in some shoots, just below nodes, brown to purplish, falcate, 3-6 mm long; prickles appear occasionally on rachis. Leaves long, 12-25 cm long. Petiole glandular. Rachis pubescent, glandular between top 1-4 pinnae. Pinnae 13-20 paired, 8-10 cm long. Leaflets 13-50 paired, 4-12 x 1.25-3.5 mm, oblong, glabrous except at base, marginal not ciliolate, lateral nerves prominant beneath, adaxial surface only midrib apparent, apex round. Inflorescence cylindrical spike, 5-12.5 cm long; peduncles 1-3 cm long, inflorescence axis pubescent; flower white, sessile. Calyx 5-lobed, 2-2.5 x 0.8 mm, densely pubescent. Corolla pubescent, 3 x 0.8 mm. Stamens glandular 4-6 mm long. Ovary 0.8 mm long; style 3.5 mm long; stipe 0.5 mm long. Pods brown to olive-brown or green, coriaceous, dehiscent, glabrous, oblong, straight, glossy, venation horizontal and extremely prominent, apex round to subacute or acuminate, 6-15 x 1.7-2.7 cm. Seeds subcircular-lenticular, 10-12 mm diam.; areole central, crescent-shaped, 3 x 4 mm; funicle 4 mm long.

Habitat: Solitary, never gregarious; found on stony hillsides on rock crevices.

Distribution: In Equatoria Mountains in South Sudan. (Found in Uganda, Congo and Ethiopia.)

Selected specimens: Equatoria, Katire, 1970, Claudio 3; 1938 Myers 8395; Abu Satta Hills, 1938, Myers 7098; Lado, 1915, Wood 1; Luluba Hills, 1938, Myers 9478; Yei, 1939, Hoyle 803. Blue Nile, Fund, 1922, Aylmer 27/16.

Observation: The pods in A. hecatophylla are glossy and the venation is very prominant. The appearance of some prickles occasionally on the internodes or even on the rachis is peculiar, but also found in A. macrostachya, thus forming the nearest allied pair of spicate species to the climbers group.

22. A. POLYACANTHA Willd. subsp. CAMPYLACANTHA (A. Rich.) Brenan in Kew Bull. 1956:195 (1956).

Arabic: Kakamut.

Type: Ethiopia, Jelajeranna, Schimper 893 (K, iso).

Syn: A. campylacantha A. Rich., Tent. Fl. Abyss. 1:242 (1847); Andrews, Fl. Pl. Sudan, 2:137 (1952).

A. caffra (Thunb.) Willd. var. campylacantha [Hochst. ex] A. Rich., Aubreville, Fl. Forest Sudno-Guin. 272 (1950).

Tree up to 25 m high. Bark yellow-brown flaking or fissured. Stem with knobby persistant prickles. Young branchlets brown to grey, pubescent. Stipules non-spinescent. Prickles in pairs just below nodes, yellow, brown or blackish or base yellow and tip black, falcate, glabrous, 0.4-1.3 cm long. Leaves 8-27 cm long. Petiole pubescent, glandular. Rachis glandular, pubescent, grooved adaxially. Pinnae 3-33 paired. Leaflets 13-60 paired, 2-6 x 0.4-1.25 mm, linear-oblong, margin ciliolate, apex obtuse to subacute. Inflorescence cylindrical spikes, 7-11.5 cm long; peduncle 0.7-3 cm long, pubescent. Flowers white-creamy, sessile. Calyx 5-lobed, pubescent, 1.8 x 0.8 mm. Corolla 5-lobed, glabrous, 3 x 0.7 mm. Stamens glandular, 5 mm long. Ovary 5 mm long; style 3.5 mm long; stipe 3 mm long. Pods brown, coriaceous, dehiscent, glabrous, oblong, 2.5-12 x 0.3-2.1 cm, apex acuminate, venation horizontal. Seeds brown, rhombic to subcircular, 7 x 7 mm; areole central, crescent-shape, 2 x 2 mm; funicle 4 mm long. Flowering August-September; fruiting December-March.

Habitat: Deciduous woodlands, riverine and groundwater forests. Usually gregarious along rivers and in rich alluvial valleys.

Distribution: South Central Sudan and the southern provinces along rivers and valleys. (Widespread in Tropical Africa from Gambia to Ethiopia in the north and to the Transvaal in the south. Also in Uganda, Kenya, Tanganyika and westwards to Ghana, Nigeria, Dahomy, Ivory Coast and Togo.)

Selected specimens: Kordofan province, El Obeid, 1970, Elamin 1419. Blue Nile, Singa, 1969, Elamin 6002. Darfur, J. Marva, 1969, Elamin 1524. Kassala, Red Sea Hills, 1966, Kassas E627. Equatoria, 1939, Andrews 906.

23. A. MACROSTACHYA Reichb. ex DC. Prod. 2:45 (1825).

Type: Senegal, Sieber (G).

Tree 5-15 m high. Bark brown. Young branchlets red-brown, tomentose with golden hairs, lenticellate. Stipules not spinescent. Prickles in pairs, under nodes, dark brown, pubescent, falcate, sometimes few or absent, 3-5 mm long. Leaves 4-12 cm long. Petiole pubescent, glandular. Rachis covered with golden hairs, glandular at top 1-4 pinnae. Pinnae 10-17 paired. Leaflets 30-35 paired, tomentose, ciliolate at margins, linear oblong, apex acute, base oblique, venation invisible, 4 x 0.7 mm. Inflorescence cylindrical spike, axis pubescent; peduncles densely pubescent, 2 cm long. Flower cream-white, sessile. Calyx pubescent, 1.5 x 0.7 mm. Corolla glabrous, pinkish, 3.5 x 0.8 mm; stamens glandular, 6 mm long. Ovary 10 mm long; style 6.5 mm long; stipe very small, 0.1 mm long. Pods dark brown coriaceous, dehiscent, oblong, pubescent, apex acuminate, venation horizontal, flat, straight, 8-10 x 2-2.7 cm, few seeds 4-5. Seeds brown, orbicular or lenticular, flattened, 7-8 mm diam.; areole central, crescent-shape, 2 x 2 mm; funicle 6.5 mm. Seeds lie vertically in pods.

Habitat: High ground in ironstone soils in high rainfall woodland.

Distribution: Southern parts of Equatoria and Bahr Elghazal Provinces in South Sudan. (Found in Senegal, Sierra Leone, Volta, Dahomy, Ivory Coast.)

Selected specimens: Bahr Elghazal, Busseri, 1931, Turner 88; Jur river, 1971, Schweinfurth 88. Equatoria, 1937, Myers 7335; Zande, 1937, Wild 257. Sudan Government 200 (unknown collector, locality and date).

Observation: Vegetative parts covered with ferrugenous hairs. In some specimens there are few scattered prickles on internodes and rachis but this character is not constant.

24. A. PERSICIFLORA Pax in Bot. Jahrb., 39:624 (1907).

Type: Ethiopia, West Shoa, Urga Valley, Rosen (BR, holo).

Syn: A. eggelingii Bak. f. in Journ. Bot. 73:263 (1935); Andrews, Fl. Pl. Sudan, 2:137 (1952).

Tree 4.5-15 m high. Bark brownish-yellow to brownish-grey, scaling off in vertical strips. Young branchlets glabrous to pubescent, with white horizontal lenticels. Stipules non spinescent. Prickles few, in pairs just below nodes, falcate, short, up to 3 mm long. Leaves 6 cm long. Petiole 1-1.5 cm, glandular. Rachis pubescent with golden hairs, 3-5 cm long, glandular between the top 1-5 pinnae. Pinnae 3-8 paired, 0.3-1 cm long. Leaflets 11-17 paired, 1.5-18 x 0.4-2.5 mm, linear-oblong, pubescent, ciliate margin, apex obtuse to subacute. Inflorescence cylindrical spike, 1.5-6 cm long; peduncle 0.3-1.8 cm long, pubescent. Flowers red or purple, sessile. Calyx red or purplish, glabrous 5-lobed, 1-1.2 x 0.8 mm. Corolla red, glabrous, 5-lobed, 2-2.5 x 0.8 mm. Stamens glandular, white, 6-8 mm long. Ovary glabrous, red, 1.2 mm long; style 6 mm long; stipe 0.1 mm long. Pods light brown, straight or slightly curved, glabrous to pubescent, coriaceous, dehiscent, venation horizontal, 6-15 x 1.4-2.5 cm. Seeds 10 in the pod, lie vertically, subcircular or lenticular, 7 x 7 mm, brown; areole central, crescent-shaped, 2 x 2 mm; funicle 6 mm long.

Habitat: Singly or gregariously in woodland and wooded grassland at an altitude of 1220-2130 m, just below stands of A. abyssinica on hill slopes.

Distribution: In tropical woodlands of South Sudan at foot of mountains in Equatoria province. (Found in Tropical Africa in Ethiopia, Uganda, Kenya, Congo.)

<u>Selected specimens</u>: Equatoria, 1950, <u>Jackson</u> 1183; Didinga Mts., 1939, <u>Myers</u> 10977; Dongotana Mts., 1941, <u>Myers</u> 14179.

<u>Observation</u>: A very distinct species by its red flowers.

25. A. ASAK (Forsk.) Willd., Sp. Pl. 4:1077 (1806).

Arabic: Assag.Beni Amer: Hag.

Type: Forskal, Hadie, Yemen (C, holo).

Syn: Mimosa asak Forsk., Fl. Aeg. Arab. 176 (1775).

A. glaucophylla [Steud.ex] A. Rich. Tent. Fl. Abyss. 1:(1847); Crowfoot, Fl. Pl. N.C. Sudan, 73 (1928); Broun & Massey, Fl. Sudan, 171 (1929); Andrews, Fl. Pl. Sudan, 2:133 (1952).

Shrub to small tree, 4-7 m high. Crown irregular. Bark of trunk grey and fissuring, on young stems and branches yellow, papery, flaky. Young branchlets pink-brown or red-brown with white streaks and horizontal slit-like lenticels, pubescent. Stipules non spinescent. Prickles in threes, two lateral straight or hooked backwards, one central hooked backwards. Leaves 2-4.5 cm long. Petiole dark brown, pubescent, glandular, 1 cm long; rachis 2-3.5 cm long, pubescent. Pinnae 4-5 paired, 2-3.5 cm long. Leaflets 10-15 paired, 4-6 x 1.5-2 mm, linear-oblong, glabrous or occasionally pubescent, margin not ciliolate, apex obtuse to subacute, midrib apparent on abaxial surface. Inflorescence cylindrical spike 4-8 cm long, glabrous axis; peduncle 0.5-1.5 cm long, pubescent. Flowers creamy-white, sessile. Calyx purple, pubescent, 2 x 1 mm. Corolla pink on midrib of lobe, glabrous, 2.5 x 0.6-0.8 mm. Stamens glandular, pink, 4-6 mm long. Ovary 1 mm long; style 5.5 mm long; stipe 0.2 mm long. Pods dark brown to pinkish brown, glabrous straight, linear, acuminate apex, coriaceous, 2.5-8 cm long, 9-12 mm wide; sparsely hairy at the stipe, venation horizontal . Seeds rhombic to lenticular, olive-green, smooth 6 x 4-5 mm; areole central, crescent-shape; funicle 3 mm long, brown.

Habitat: Has a unique habitat amongst the Acacias in growing in cracks of rocks in the Red Sea Hills.

Distribution: Red Sea Hills of Eastern Sudan. (In Africa it is found in Ethiopia, Somaliland, and extends to Arabia. Thus it is a typical North-East African species.)

Specimens cited: Kassala, J. Gamal, 1970, Elamin & Elsheikh 1656. Red Sea Hills, Kassas & Obeid E151; Red Sea Hills, 1966, Kassas & Obeid E67; Kassala, 1907, Broun 1039; Karora Hills, 1923, Crowfoot s.n.; Khor Taqqat, 1936, Cooke B.K.C. 195; Jebel Kassala, 1959, Jackson 3914; Suakin, 1868, Schweinfurth 89; Red Sea Hills, 1928, Newsberry 104.

26. A. SENEGAL (L.) Willd. var. SENEGAL; Brenan, Fl. Trop. East Afr., 93 (1959).

Arabic: Hashab.

Type: Unknown.

Syn: Mimosa senegal L., Sp. Pl. 521 (1753).

A. verek Guill. et Perr. in Fl. Seneg. Tent. 1:245, t. 56 (1832); Crowfoot, Fl. Pl. N. C. Sudan 73 (1928); Broun & Massey, Fl. Sudan, 171 (1929).

A. senegal (L.) Willd., Sp. Pl. 4:1077 (1806); Andrews, Fl. Pl. Sudan, 2:135 (1952).

Shrub to small tree 2-12 m. Bark yellow to light brown or grey, rough, fissuring or flaking. Young branchlets grey, yellow or brown, pubescent to glabrous, with horizontal slit-like lenticels. Stipules not spinescent. Prickles at nodes, in threes, 2 lateral pointing upward or forward and one central pointing downward or backward, falcate, dark brown with a grey base, 4-7 mm long. Leaves 1-6 cm long. Petiole glandular, 0.3-0.6 cm. Rachis pubescent and glandular between the end 1-5 pinnae. Pinnae 2-6 paired, 0.5-3 cm long. Leaflets 8-18 paired, 1-7 x 0.5-2 mm, linear to elliptic-oblong, ciliolate on margins, glabrous or pubescent, apex obtuse to subacute. Inflorescence cylindrical spike, 2-10 cm long, on peduncles 0.7-2 cm.long, pubescent or glabrous. Flowers white or cream, sessile. Calyx pubescent, 2 x 0.7 mm, 5-6 lobed, creamy or pinkish. Corolla glabrous, cream, 2.5 x 0.3 mm. Stamens glandular, 4-7 mm long. Ovary glabrous 0.7 mm long; style 4.5 mm long; stipe 0.2 mm long. Pods pale brown to straw-colour, membranous, dehiscent, pubescent, flat, straight, oblong, apex rounded to acuminate, 3-14 cm long, 1-3.3 cm wide. Seeds orbicular 8-12 mm diam., yellow or pale brown, compressed; areole central, crescent-shaped, 1.5-6 x 2.5-5 mm; funicle 7.5 mm long. Seeds lie vertically on pods. Flowering November-February; fruiting January-April.

Habitat: On sandy and clay plains of savanna grasslands.

Distribution: Central Sudan, a continuous belt from east to west, though more successful on the western sand plains of Kordofan and Darfur; pure or mixed with A. mellifera. The rainfall ranges from semi-desert type, 75 mm, up to 800 mm on savanna woodlands. (Widespread in Tropical Africa.)

Selected specimens: Kordofan, El Haraza, 1970, Elamin 1604; El Idaya, 1970, Elamin 1553. Darfur, Kondowa, 1969, Elamin 2291; Radom, 1970, Elamin 1503. Blue Nile, Singa, 1969, Elamin 2291. Kassala, 1970, Elamin 3211.

Observation: Gum Arabic of commerce is produced from this species. It is very variable in characters. Its nearest relative in the Sudan is A. asak, both having the 3 prickles, but they are separated by habitat, pod characters and the direction at which the two lateral prickles are pointing.

27. A. ATAXACANTHA DC., Prod. 2:459 (1825).

Type: Senegal, Bacle (G-DC, syn) & Perrottet (Edin. syn!).

Scandent shrub, 10-15 m high, solitary or forming a thicket. Bark grey flaking. Young branchlets pubescent, brown, furrowed. Stipules not spinescent, foliate. Prickles, falcate, scattered on branches, on internodes, and on leaves rachis and pinnae, pubescent, dark brown, up to 1 cm long. Twigs with white horizontal lenticels. Leaves 10-15 cm long. Petiole glandular and pubescent. Rachis pubescent, prickly, gland before first pinnae and uppermost 1-5 pairs of pinnae. Pinnae 10-25 paired. Leaflets 14-50 paired, 2-8.5 x 0.5-2.5 mm, surface glabrous, margin ciliolate, linear oblong, apex obtuse to subacute, venation not visible. Inflorescence cylindrical spikes, peduncles 1-2.5 cm long, pubescent. Flowers white to cream, pedicellate 0.25-0.5 mm long. Calyx 1-1.7 mm long, glabrous to pubescent. Corolla 5-lobed, 1.5-3 mm long. Stamens 3-6 mm long, shortly connate at the base up to 1 mm; ovary dark green to brown, densely pubescent, on a stipe longer than ovary. Ovary 9 mm long; style 2.1 mm long; stipe 1-5 mm long. Pods brown to purplish-brown, linear oblong, dehiscent, straight, acuminate at both ends, glabrous, 5-15 cm long, 1-1.9 cm wide. Seeds 4-6 per pod, orbicular or lenticular, brown to greenish-brown, compressed, 6-7 mm diam.; areole central, crescent-shape, 2.5-3 x 2.5-3 mm; funicle yellow-brownish, 7 mm long. Seeds lie longitudinally or obliquely in the pods. Flowering May-August; fruiting September-October.

Habitat: On light silty soils in riverine forest and thicket.

Distribution: Usually in high rainfall areas of the southern provinces, but also around J. Marra and Kuttom in Darfur Province. (In Africa from

Senegal to Ubango-Shari, Kenya, Tanganyika, to South Rhodesia and Portuguese East Africa, southwards to Angola, South Africa and South-West Africa, westwards to Ghana, Nigeria and Dahomy.)

Selected specimens: Darfur, J. Marra, 1921, Lynes 562; Garsilla, 1964, Wickens 1604; Gildu, 1957, Francis 28; Zalingi, 1964, Wickens 2742; Huntegello, 1969, Elamin 1546; J. Marra, 1939, Dandy 42.

28. A. BREVISPICA Harms in Notizbl. Bot. 8:370 (1923).

Type: Tanganyika, Lushoto District, Kitivo, Holst 606 (B, holo).

Syn: A. pennata auct. non (L.) Willd.; Broun & Massey, Fl. Sudan, 173 (1929), p.p.; Andrews, Fl. Pl. Sudan, 2:150 (1952), p.p.

Climber 1-7 m high, often semi-scandent. Bark smooth, grey. Young branchlets pubescent with minute reddish glands. Stipules not spinescent, foliate. Prickles scattered, 2-3 mm long, on stems arising from longitudinal bands along the stem which are usually paler than the intervening lenticellate bands; branches brown red or grey-brown with yellow-whitish horizontal slit-like lenticels. Leaves 5.5-10 cm long. Petiole 0.5-0.8 cm long, glandular, pubescent. Rachis 3.5-5.5 cm, pubescent, prickly and glandular on the uppermost 1-3 pinnae. Pinnae 6-18 paired, 1-4 cm long. Leaflets 20-35 paired, linear or linear oblong, 2-3 mm long, 0.5-0.8 mm wide, lower surface usually appressed silky puberulous, sometimes glabrous, margins conspicuously appressed, puberulous. Inflorescence capitate; peduncles pubescent, 1.5-2.2 cm long; involucel on lower half of peduncle. Flower white to cream or yellowish, sessile. Calyx 5-6 lobed, pubescent, dark at apex and base, 2.5 x 0.7 mm. Corolla, 5-6 lobed, dark tips and bases, glabrous, 3 x 0.8 mm. Stamens free, glandular, 4 mm long; anthers dark pink. Ovary dark brown, pubescent, 1 mm long; style 3 mm long; stipe longer than ovary, 1.5 mm long. Pods brown, pubescent, with red glands or glabrous, linear oblong, straight, 6-15 x 1.5-3.3 cm, venation horizontal, 8 seeds to the pod. Seeds brown, smooth, elliptic or obovate, glabrous, 6-13 x 6-8 cm; areole marginal, U-shaped, 3.5-6 x 2-3 mm; funicle dark brown, pubescent, 5-9 mm long. Flowering June-November; fruiting December-February.

Habitat: In bushlands, thicket, scrub in tropical high rain areas and on dry rocky slopes.

Distribution: In Southern Equatoria and Bahr Elghazal Provinces. (Found in East Africa in Ethiopia, Somaliland, Tanganyika, Uganda, Kenya to the Congo and Portuguese East Africa, southwards to Angola, and South Africa, westwards in Ghana, Siera Leone and Ivory Coast.)

Selected specimens: Equatoria, Didinga Mts., 1949, (collector unknown) 673; Didinga Mts., 1950, Jackson 1296; Didinga Mts., 1939, Myers 10869; Didinga Mts., 1940, Myers 13469.

29. A. SCHWEINFURTHII Brenan & Exell var. SCHWEINFURTHII; Brenan & Exell in Bol. Soc. Brot. 2(3):128 (1957).

Type: Sudan, Gubbiki, Schweinfurth 2206 (B.M., holo! K, iso!).

Syn: A. pennata auct. non (L.) Willd.; Broun & Massey, Fl. Sudan, 173 (1929) p.p.; Andrews Fl. Pl. Sudan 2:150 (1952), p.p.

Climber, 10-14 m high, straggling bush when no trees are available. Branches olive-green or pale brown, grooved longitudinally with dark and pale bands alternating longitudinally, pubescent with red glands. Stipules non spinescent, foliate. Prickles scattered falcate, arising from brown longitudinal bands darker than the intervening yellowish to grey ones. Leaves 16-18 cm long. Petiole 3-6 cm long, glandular. Rachis pubescent up to 18 cm long, glandular at uppermost 1-3 pinnae. Pinnae 9-17 paired, 6-9 cm long. Leaflets 40-60 paired, linear oblong, 6 x 0.5 mm, glabrous, margins with appressed white hairs, apex subacute. Inflorescence capitate; peduncle 1-1.3 cm long, densely pubescent; involucel at base of peduncle. Flower white to cream, sessile. Calyx pubescent 2 x 0.5 mm, 5-lobed. Corolla pubescent 3 x 0.5-6 mm, 5-lobed. Stamens connate in a short tube, 1 mm long, glandular 6.5 mm long. Ovary densely pubescent, 0.6 mm long; style 2.5 mm long; stipe hairy, 8 mm long. Pods coriaceous, oblong, transversely plicate and umbonate over the seeds, light brown. Seeds blackish or dark brown, 9-11 x 6.8 mm, smooth, elliptic; areole marginal U-shaped; funicle 6 mm long. Flowering June-November; fruiting December-January.

Habitat: On light alluvial soils in riverine forests and deciduous woodlands.

Distribution: In tropical rain forests along rivers in Bahr Elghazal and Equatoria Provinces in South Sudan. (Found in Tenganyika and southwards to Portuguese East Africa and South Africa.)

Selected specimens: Bahr Elghazal, Wau, 1970, Latif 87; Jur river, 1931, Turner 86. Equatoria, Gubbiki, 1869, Schweinfurth 2206; Bahr El Jebel, 1929, Simpson 7270.

30. A. PENTAGONA (Schumach. & Thonn.) Hook. f. in Niger Fl. :331 (1849).

Type: Ghana, Jadofa, Thonning (C, holo, K, photo!).

Syn: Mimosa pentagona Schumach. & Thonn., Beskr. Guin. Pl. :324 (1827).

A. pennata auct. non (L.) Willd.; Broun & Massey, Fl. Sudan 173 (1929) p.p.; Andrews, Fl. Pl. Sudan (1952), p.p.

Climber up to 12 m high; stem dark brown or purplish; branches pubescent to glabrous, eglandular, or rarely with inconspicuous red-brown or purplish glands, dark and pale bands alternating. Stipules non spinescent, foliate. Prickles scattered on dark bands of branches, falcate. Leaves up to 18 cm long. Petiole 1.5-6 cm, glandular; rachis pubescent glandular. Pinnae 15-20 paired, 2.5-9 cm long. Leaflets 20-65 paired, linear oblong, 0.7-2 mm wide, glabrous, apex round, midrib apparent on both sides. Inflorescence capitate peduncles 1-1.3 cm long, pubescent; involucel at base of peduncle. Flowers white, sessile. Calyx 2.5 x 0.7 mm, 5-lobed. Corolla 3 x 0.7 mm, 5-lobed. Stamens glandular, 5 mm long. Ovary 10 mm, glabrous; style 2.5 mm long; stipe 12 mm long, glabrous, longer than ovary. Pods oblong, thick, hard, dark brown, 7.5-16 cm long, 1.8-3.5 cm wide; 6-7 seeds in the pods, glabrous, umbonate over the seeds, venation horizontal. Seeds brown or dark brown to black, smooth, ellipsoid, thick, but somewhat compressed, 10-13 x 6-8 mm; areole U-shaped, marginal, 7-10 x 4.5-6 mm; funicle 5-6 mm long. Flowering June-November; fruiting December-January.

Habitat: In high rainfall woodland forests on river banks.

Distribution: Southern borders of the Sudan and Congo in tropical woodland forests in South-West Equatoria province. (In Africa from French Guinea and Sierra Leone to the Belgian Congo, Uganda, Kenya, Tanganyika, southwards to Angola, Rhodesia, and Portuguese East Africa.)

Selected specimens: Equatoria, Lande, 1870, Schweinfurth 3363; Zandeland, 1941, Wyld 845.

31. A. ALBIDA Del., Fl. Aeg. :142 t. fig. 3 (1813).

Arabic: Haraz.

Type: Egypt, above Philae, Nectoux (MPU, holo).

Syn: Faidherbia albida (Del.) A. Chev. in Rev. Bot. Appliq. 14:876 (1934).

Large tree up to 30 m high. Crown round or spreading. One main stem, buttressed or not. Bark brown or dull grey. Young branches ashen to whitish, pubescent or glabrous, zigzag pattern, smooth or fissured to expose a green cortex. Stipules spinescent. Spines at nodes, straight, brown with white base, 0.9-2.3 cm long; galled spines and other prickles absent. Leaves 7-10 cm long. Petiole eglandular, pubescent, brown, 1 cm long. Rachis green, pubescent, grooved, glandular between every pinna pair, 6-9 cm long. Pinnae 2-10 paired, 2-3 cm long, glands present between leaflet pairs also. Leaflets 6-23 paired, 2.5-12 x 0.7-4 mm, apex round, subacute or mucronate, pubescent and ciliolate margins, venation visible on abaxial surface, oblong-linear or slightly obovate. Inflorescence cylindrical spikes, white to cream, 3.5-15 cm long; peduncles pubescent, 1.3-4 cm long. Flowers sessile to pedicellate, 0.5-2 mm long. Calyx 5-lobed, pubescent, 1-2.5 mm long. Corolla pubescent, 3-4.5 mm long; stamens united up to 1 mm up the base, eglandular, 4-5 mm long. Ovary glabrous, brown, 2 mm long; style glabrous, 7.5 mm long; stipe 0.7-1.4 mm long. Pods bright orange, falcate, curled or spiral, indehiscent, pulpy, apex round or acute, glabrous or rarely pubescent, red glands on pod surface, margin entire, no seed constrictions, venation longitudinal or not visible, 6-25 x 1.8-5 cm. Seeds 11-29 to the pod, lie vertically inside pods, obovate, 9-11 x 6-8 mm, brown; areole U-shaped or O-shaped, marginal, 7-9 x 4-6 mm; funicle 4 mm long. Flowering November-

January; fruiting December-April.

Habitat: Wide range of habitats, ranging from the alluvial soils of perennial or seasonal watercourses, to open savanna woodland and cultivated land. They occur singly or gregariously.

Distribution: Widely spread in Sudan along rivers, streams and water depressions from south to north and east to west. Successful along the seasonal watercourses of Western Sudan in Darfur province. (Also widely spread all over Africa from Egypt, Senegal and Gambia, southwards to South Africa and all over East and West Africa. Its distribution extends northwards to Syria and Palestine.)

Selected specimens: Khartoum, Forest reserve, 1969, Elsheikh 1433. Darfur, J. Marra, 1969, Elamin 1550; Kondowa, 1970, Elamin 1565. Blue Nile, Singa, 1969, Elamin 6352. Bahr Elghazal, Niamlelle, 1969, Elamin 4520.

This species, and its generic position, is discussed more fully at end of Chapter III.

A. Sp. Nov.?

In North Lorienatom in South-East Sudan.

The specimen was collected by I. R. Dale, No. S303 (1943) and placed in the East African Herbarium in Nairobi (Kew, Negative No. 3264).

I have seen the photo of this specimen at Kew, showing broad leaflets like A. mellifera but more than 4 pinnae; no inflorescence or pods were seen, and it is difficult to relate it to any of the existing species.

4. DISTRIBUTION AND ECOLOGY OF THE ACACIAS IN THE SUDAN

Distribution and habitat factors were mentioned briefly under individual species in the previous notes. Maps of distribution of the studied species are produced here to show the localities of the collected specimens and the known distribution of the species in the Sudan, which is a result of the writer's observation in the field, in addition to the available literature on the subject. (See Maps 5-43, page 212-221) A study of certain leaf characters has been made to investigate the correlation of morphological and ecological features.

Distribution

The Sudan may be divided into three major ecological zones.

The first zone is Northern Sudan, with desert and semi-desert conditions (rainfall 0-200 mm). The Central Sudan zone includes the savanna, clay and sandy plains of Central Sudan (rainfall 200-750 mm); the south-eastern corner of the Sudan, known as Tobosa, is included in this ecological zone. Finally the Southern Sudan zone (rainfall 750-2000 mm) includes the broad-leaved forests of Southern Sudan with tropical rain forests, especially at the southern border with Uganda and Congo.

The Acacia species present in Northern Sudan are the following : A. ehrenbergiana, A. tortilis, A. seyal, A. nilotica, A. albida, A. etbaica, as typical species of Northern Sudan, but other species of the central zone do occur at the southern extremities of the northern zone, e.g. A. nubica, A. senegal, A. mellifera, A. laeta and probably A. asak.

The Acacia species present in Central Sudan are:

A. seyal, A. drepanolobium, A. gerrardii, A. albida, A. nilotica, A. senegal, A. mellifera, A. laeta, A. asak. The Tobosa area in South-Eastern Sudan has the following species: A. horrida, A. reficiens, A. paolii and A. elatior.

The Acacia species found in Southern Sudan are : A. brevispica, A. schweinfurthii, A. pentagona, A. polyacantha, A. hecatophylla, A. macrostachya, A. abyssinica, A. macrothyrsa, A. dolichocephala, A. hockii, A. kirkii, A. ataxacantha, A. sieberana.

This is the general distribution of the Sudan species in the three ecological zones, but it must be mentioned that a few species can occur outside their zone in an adjacent ecologically related zone, e.g. A. senegal, A. mellifera and A. laeta, all of Central Sudan, also extended into the southern borders of the Northern Sudan zone; whereas A. sieberana, A. polyacantha and A. ataxacantha occur on the southern borders of Central Sudan, but always in ecologically modified areas like Jebel Marra and the Nuba Mountains in Southern Kordofan.

Another distributional fact emerges. There is a dominance of members of Group I in the Northern Sudan, a mixture of Groups I and II in Central Sudan zone, and a dominance of Groups II and III in Southern Sudan. In Northern and Central Sudan individual species of Group I cover a wide area together with two species of Group II, namely A. mellifera and A. senegal. This indicates that Acacia species are well adapted to the ecological conditions in Central and Northern Sudan. The Southern Sudan contains a larger number of species, yet the areas occupied by individual species are comparatively small and restricted to special habitats for every species, e.g. the special montane habitats of A. abyssinica and A. hecatophylla, and the special tropical forests habitats of A. brevispica and A. macrothyrsa.

As one goes northwards in Central and Northern Sudan, the species tend to have broad distributional belts running west and east of the Nile, like that of A. senegal, A. mellifera, A. nubica and A. seyal. These Acacia belts do not exist in the Southern Sudan, where instead we get species like A. horrida, A. paolii, A. reficiens and A. elatior, which all exist in South-Eastern Sudan but never cross the Nile to the western parts. A. abyssinica and A. hecatophylla also are not reported west of the Nile. The reason for the presence of the broad belts in Central and Northern Sudan is due to the light-demanding nature of the Acacia species. The Central and Northern Sudan consists of open grassland with few big crowned trees and such conditions are suitable for the growth of Acacias; in the Southern Sudan, on the other hand, there are closed multi-storeyed forests, and the Acacias have to fight very hard to shoot up for light.

Animals, especially domestic ones, are the major factor of seed dispersal of the Acacias. In Central and Northern Sudan, the animals eat the Acacia pods in the dry season and the seeds are passed in the dung after being softened by the stomach acids. This process helps in the dispersal of the seeds in wide areas and softens the testas, which will be ready to germinate with the coming rains. Domestic animals are lacking in the unsuitable environments of Southern Sudan.

Another factor favouring the wide spread of Acacia species in Northern and Central Sudan is the annual grass fires which occur throughout the dry grass savanna plains. I have noticed that the seeds of A. seyal germinate successfully only when there is a grass fire in the area; these fires break the seeds' testa and make them ready for germination with the coming rains. It is most probable that the same fire effect applies to other species in the dry savanna zone. In Southern Sudan the conditions for grass fires do not exist.

Most of the Acacia species are concentrated in Southern Sudan and specifically east of the Nile; the number of species in this area is 17, compared with 14 species in Central and Northern Sudan. This distributional pattern gives an indication of the centre of diversity of the Acacias in the Sudan as being in the south-eastern part, where the genus has its maximum morphological diversity and has probably radiated to other parts of the Sudan. From this centre of diversity and radiating westwards, distribution is hampered by the thick closed forests and hence the failure for the genus to occupy large areas in South-Western Sudan. The radiation northwards was successful because of the open savanna and hence the success of the genus in Central Sudan.

Another interesting feature of Acacia distribution is the pattern of belts parallel to the Nile and its tributaries. Starting from the southern borders of Central Sudan and going northwards to the Egyptian border, is a belt of A. nilotica in the silty banks of the Nile, then one of A. albida in the higher, less silty, ground, and finally a belt of A. seyal on the highest clay grounds away from the banks. Going southwards from the southern borders of Central Sudan the A. nilotica belt is replaced by A. sieberana, and then further southwards, the two belts of A. albida and A. seyal are replaced by A. polyacantha subsp. campylacantha.

There are two species, A. etbaica and A. asak growing on the Red Sea Hills and always associated together. These two species, though existing

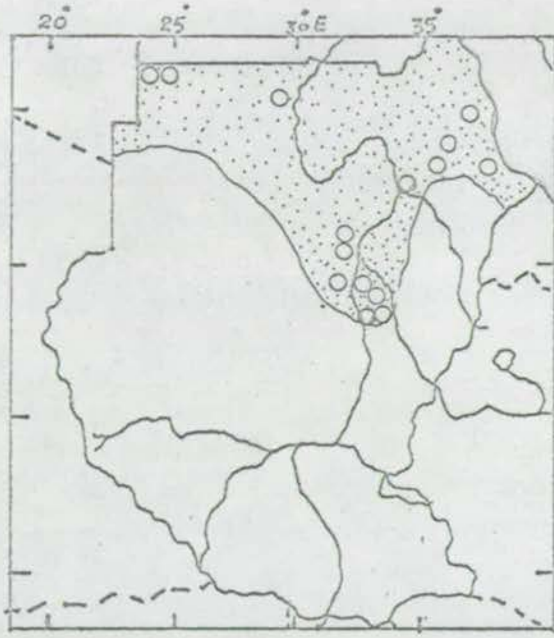
Distribution maps of Acacias in the Sudan

Maps 5-43. Distribution of Acacia species, subspecies and varieties in the Sudan.

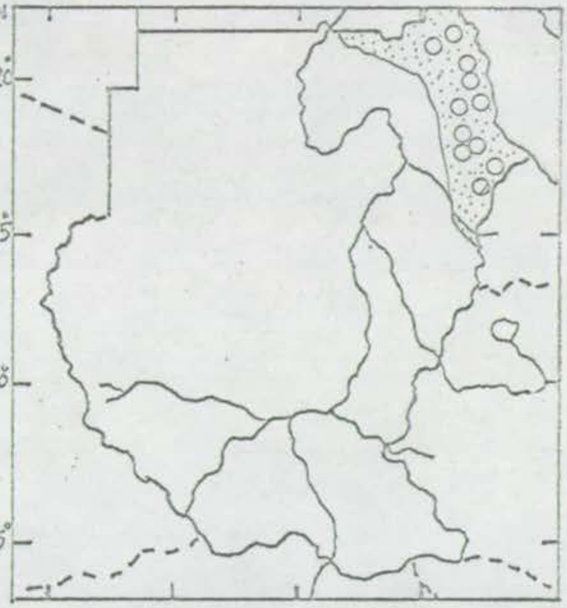
Circles indicate cited specimens.

Dots indicate the range of the taxon based on specimens not cited in this account, field observations and literature records.

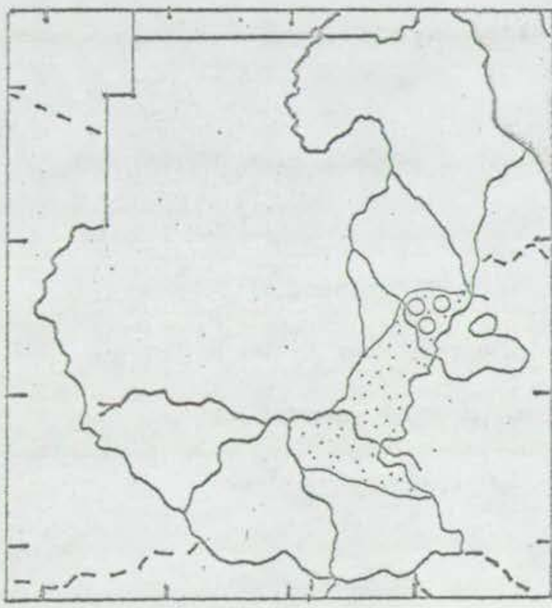
SCALE



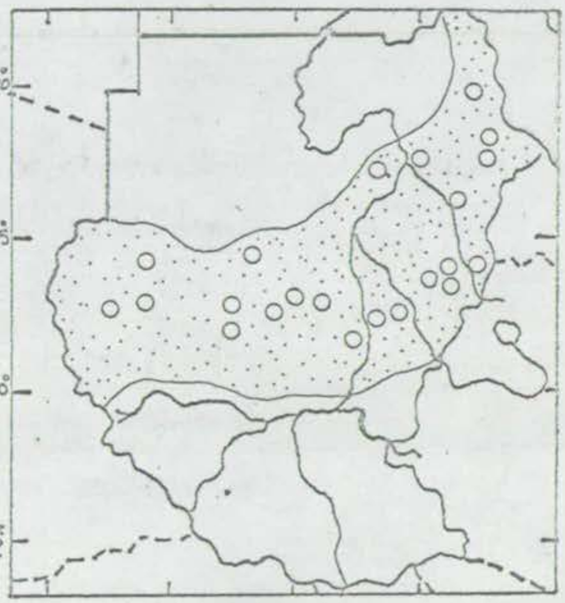
5. A. EHRENBERGIANA



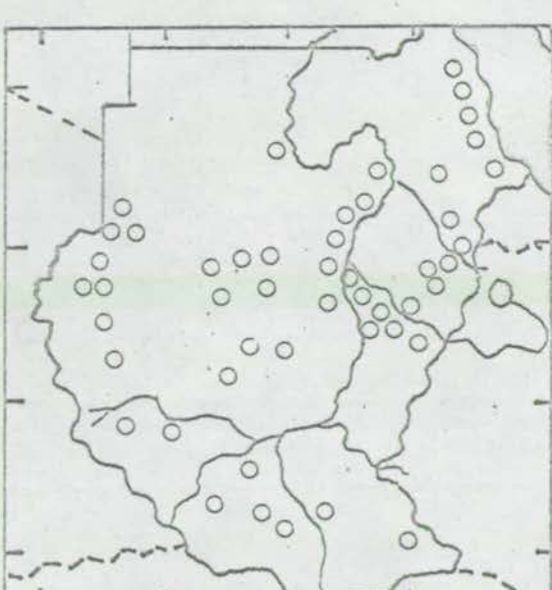
6. A. ETBAICA SUBSP. ETBAICA

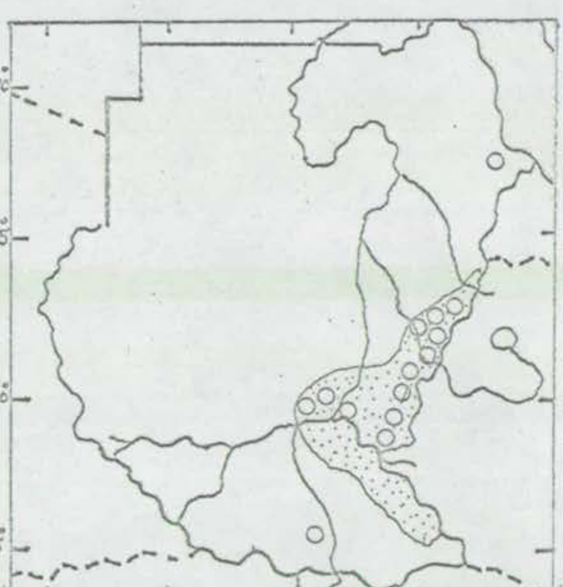


7. A. DREPANOLOBIUM



8. A. NUBICA

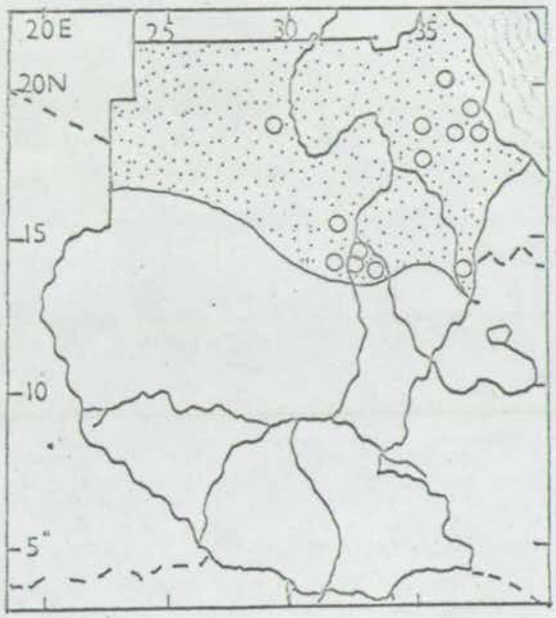




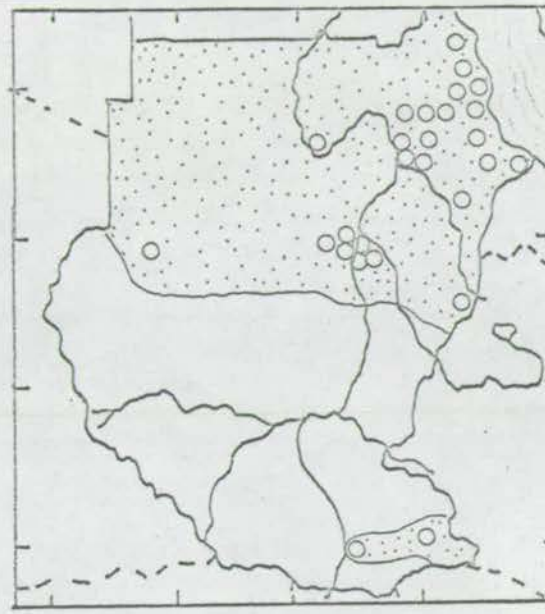
9. A. SEYAL VAR. SEYAL

10. A. SEYAL VAR. FISTULA

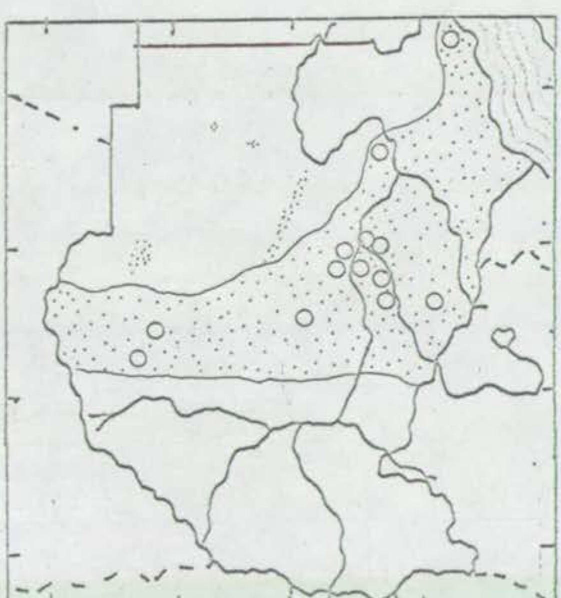
SCALE : 500 KILOMETRES.



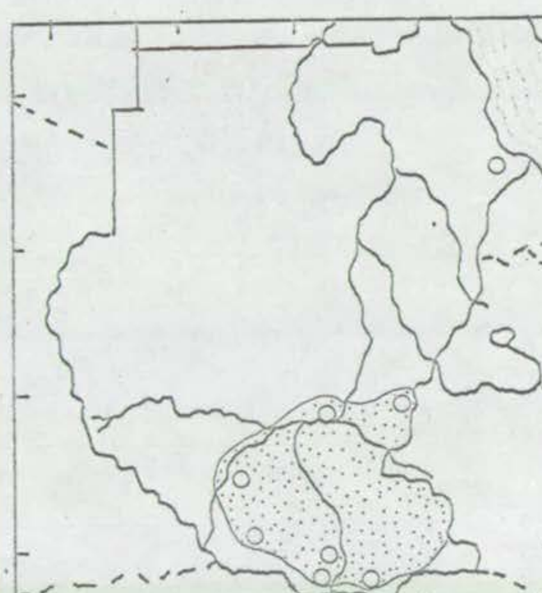
11. A.TORTILIS SUBSP. TORTILIS



12. A.TORTILIS SUBSP. SPIROCARPA

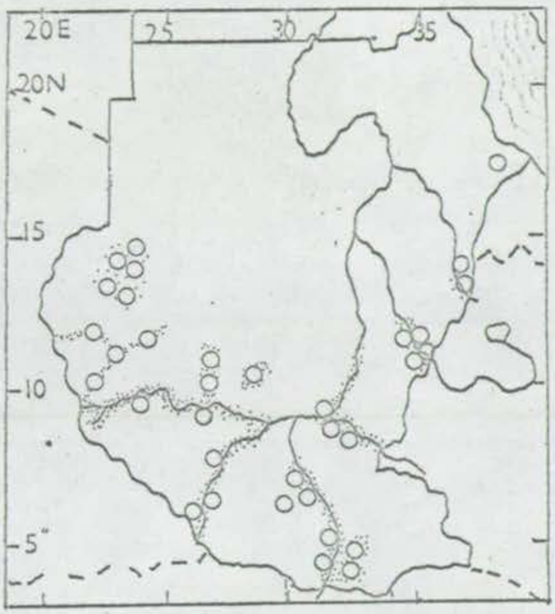


13. A.TORTILIS SUBSP. RADDIANA

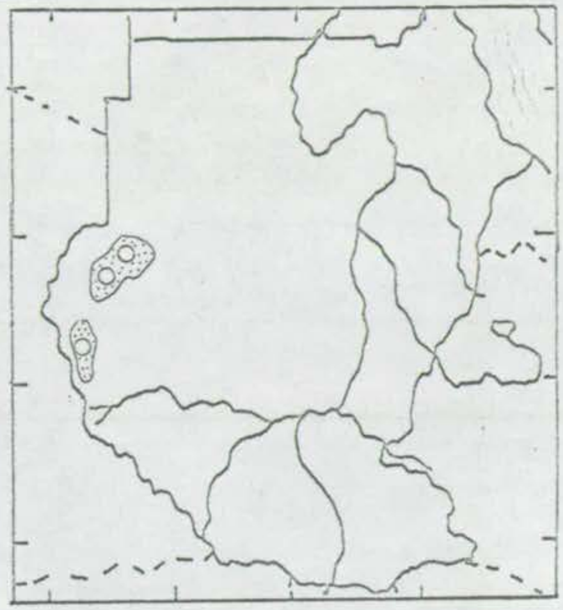


14 A. HOCKII

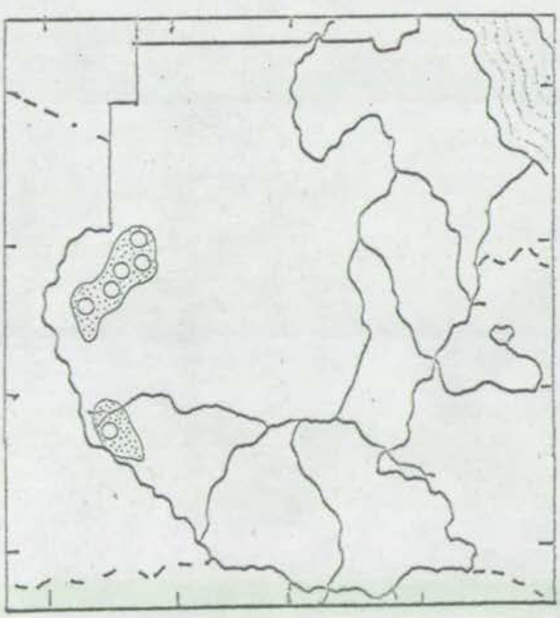
SCALE : 500 KILOMETRES.



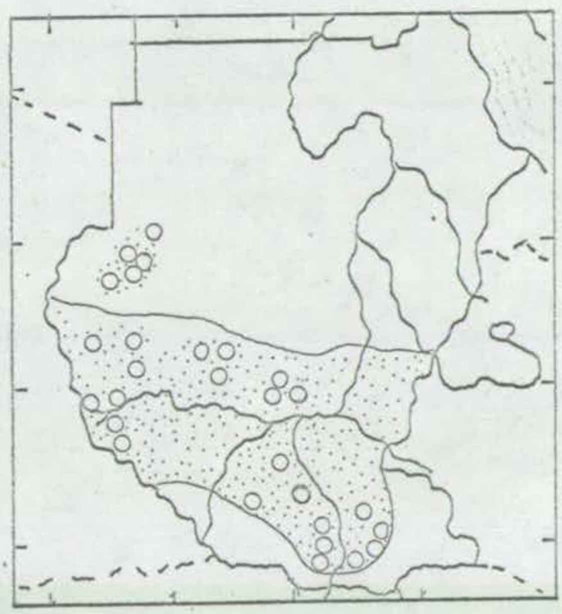
15. A. SIEBERANA VAR. SIEBERANA



16. A. SIEBERANA VAR. VILLOSA

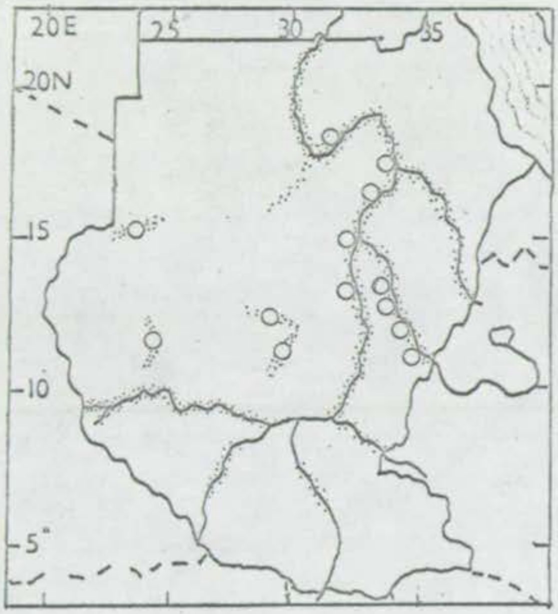


17. A. SIEBERANA VAR. VERMOESENII

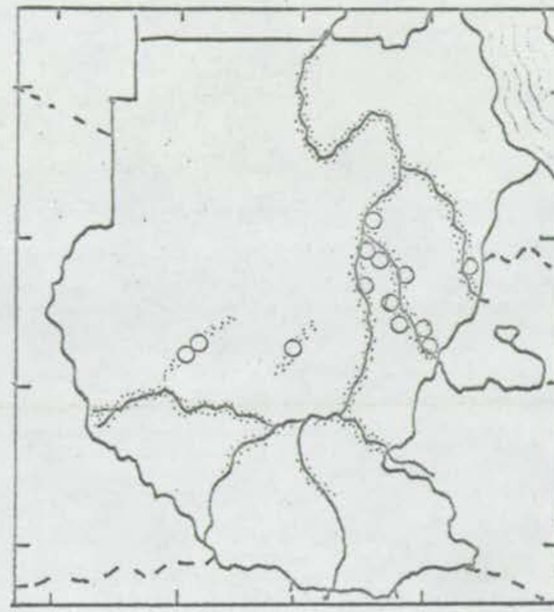


18. A. GERRARDII VAR. GERRARDII

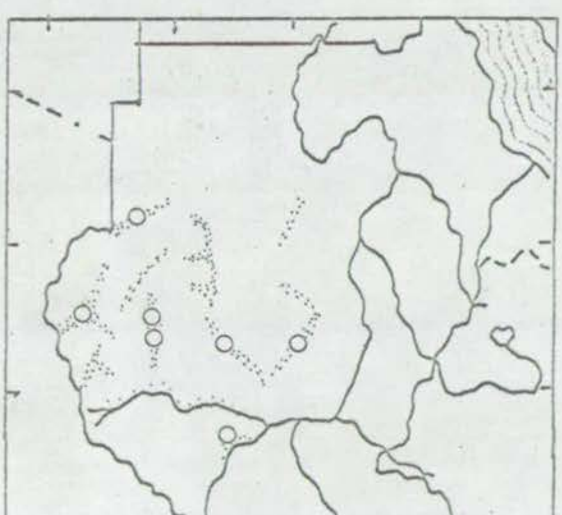
SCALE : 500 KILOMETRES.



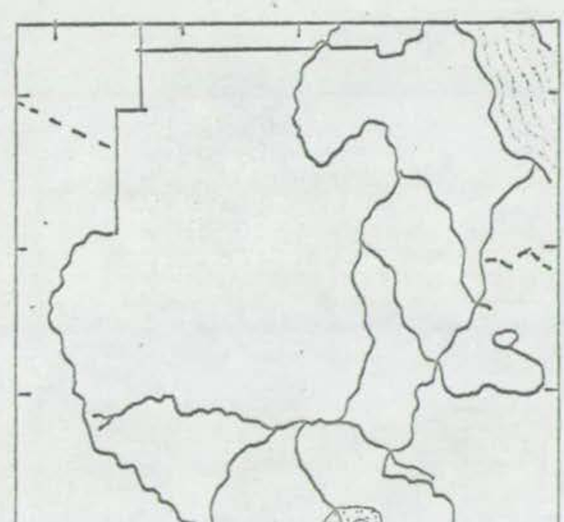
19. A. NILOTICA SUBSP. NILOTICA



20. A. NILOTICA SUBSP TOMENTOSA

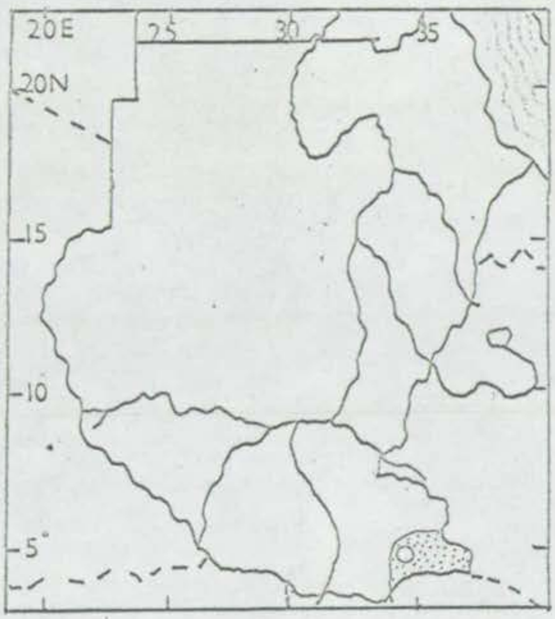


21. A. NILOTICA SUBSP ASTRINGENS

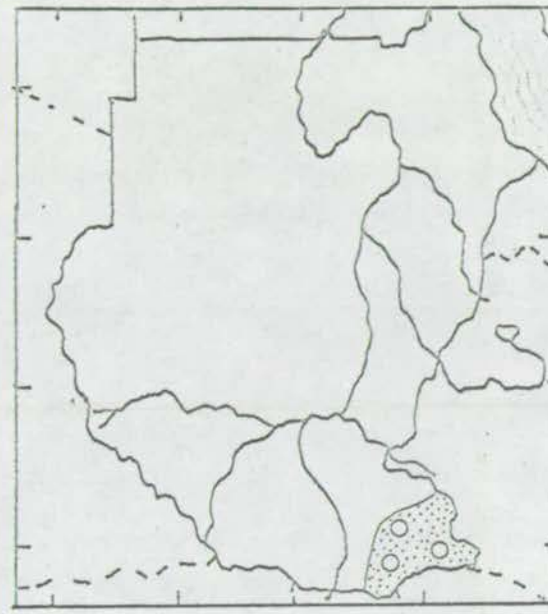


22. A. NILOTICA SUBSP SUBALATA

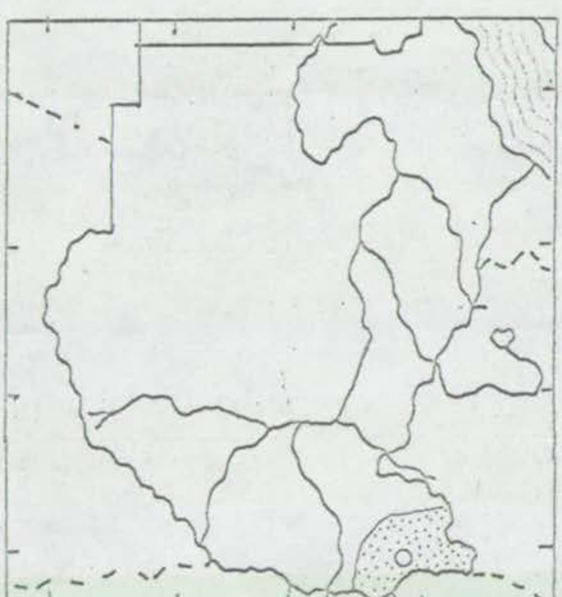
SCALE : 500 KILOMETRES.



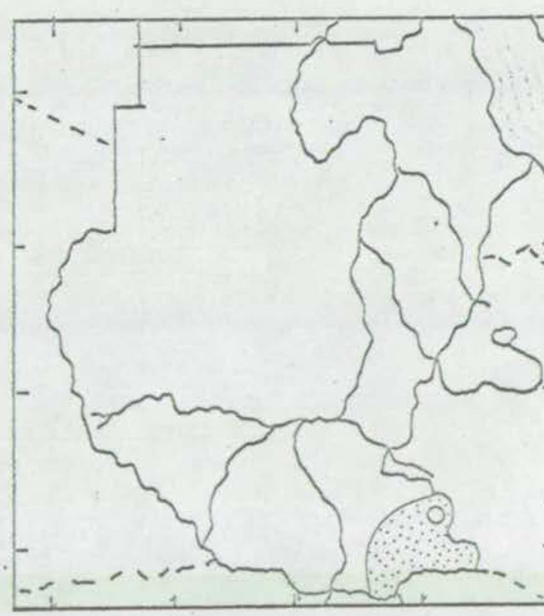
23. A. PAOLII



24. A. REFICIENS SUBSP. MISERA

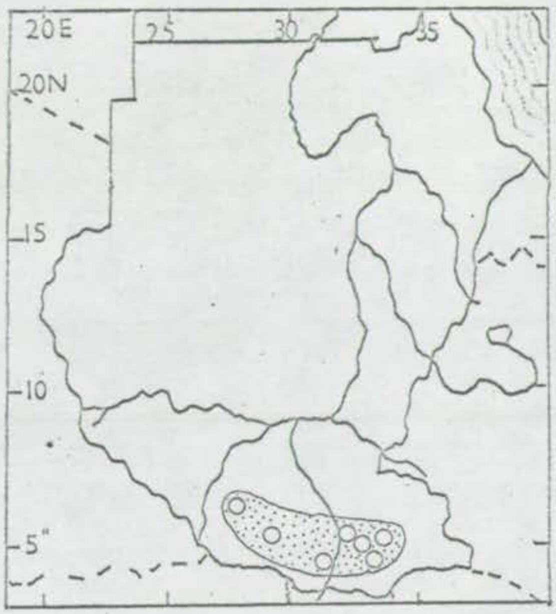


25. A. ELATIOR SUBSP. TURKANAE

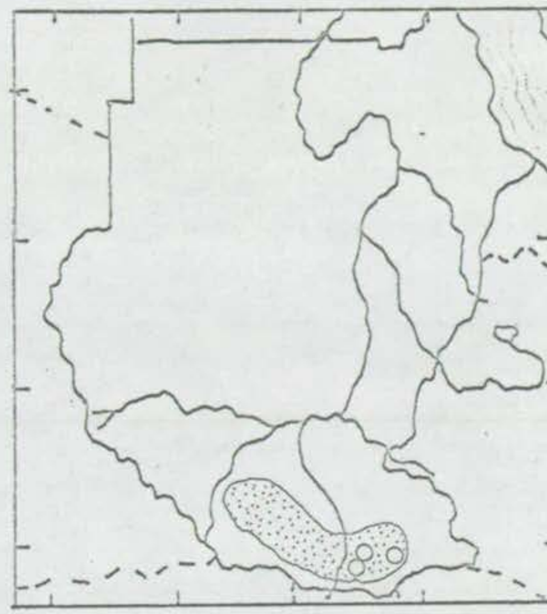


26. A. HORRIDA SUBSP. BENADIRENSIS

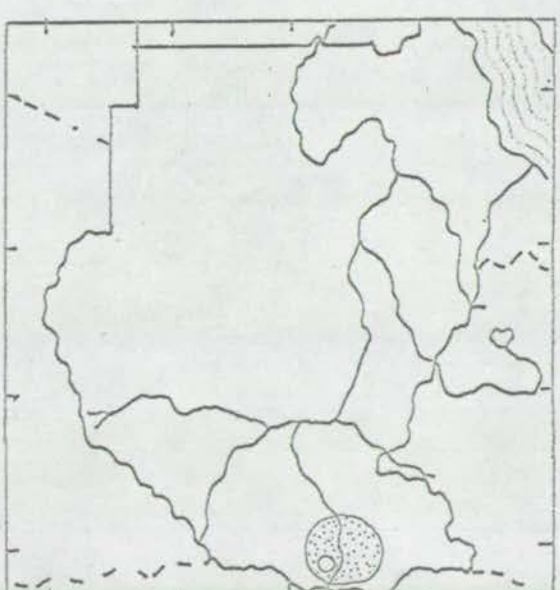
SCALE : 500 KILOMETRES.



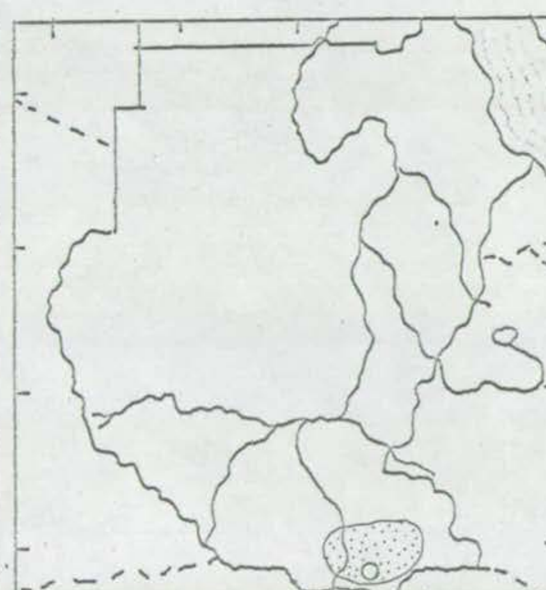
27. A. MACROTHYRSA



28. A. ABYSSINICA SUBSP. CALOPHYLLA

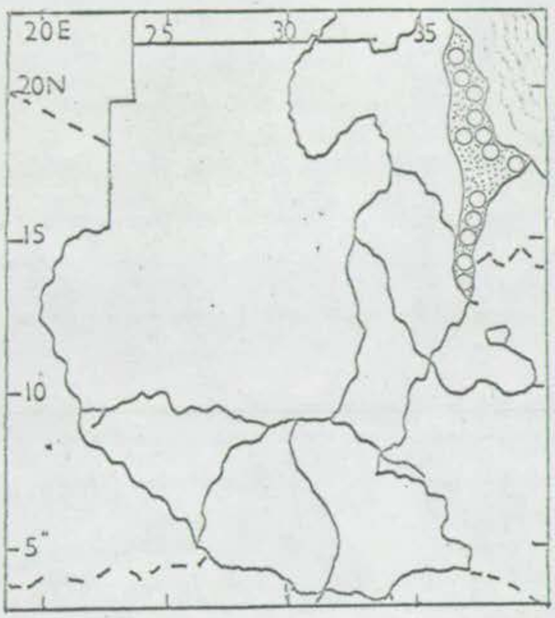


29. A. KIRKII SUBSP. MILDBRAEDII

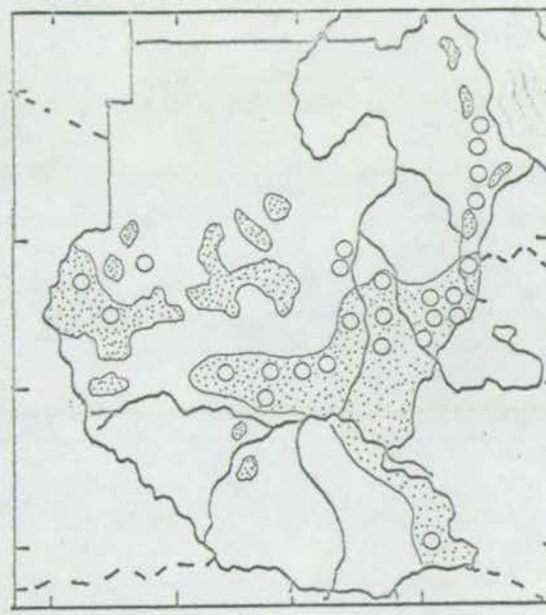


30. A. DOLICHOCEPHALA

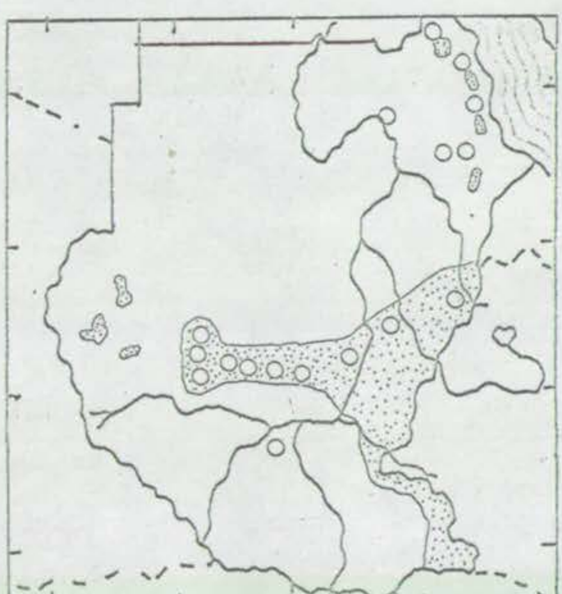
SCALE : 500 KILOMETRES.



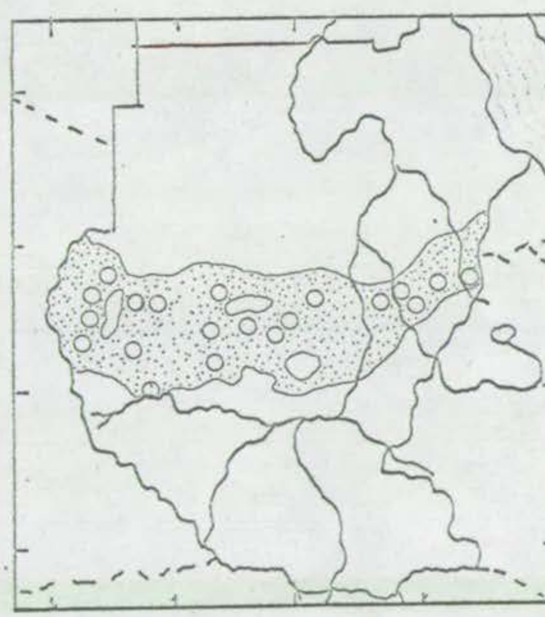
31. A. ASAK



32. A. MELLIFERA SUBSP. MELLIFERA

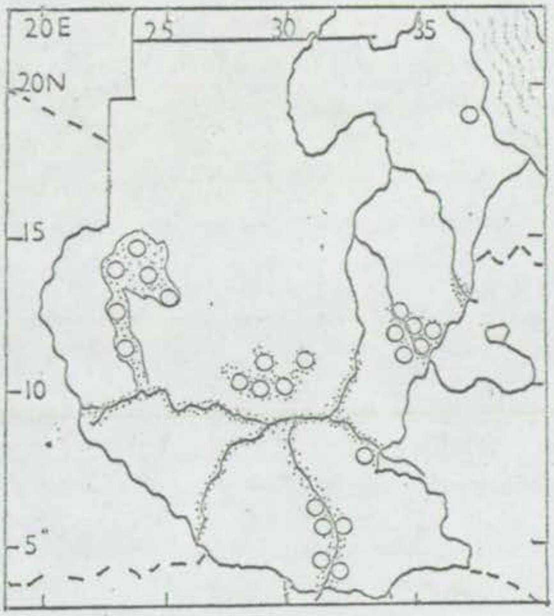


33. A. LAETA

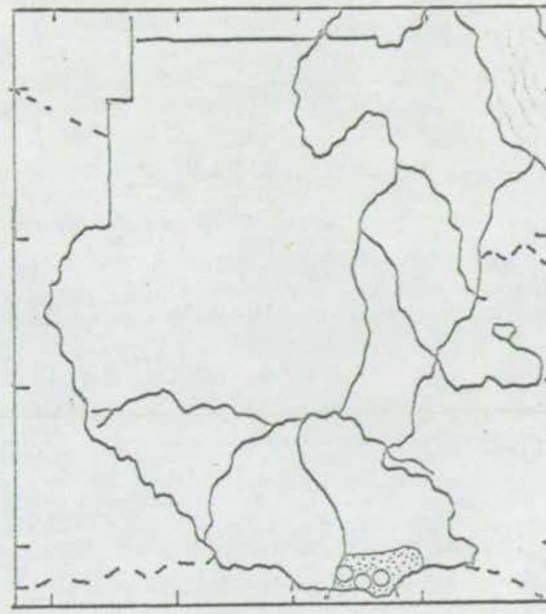


34 A. SENEGAL

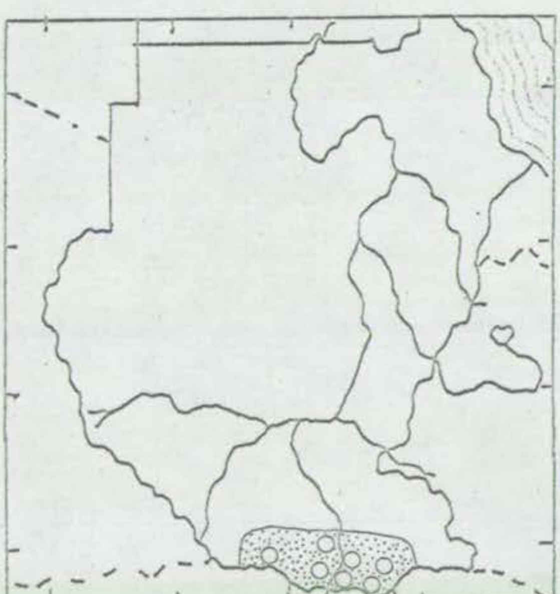
SCALE : 500 KILOMETRES.



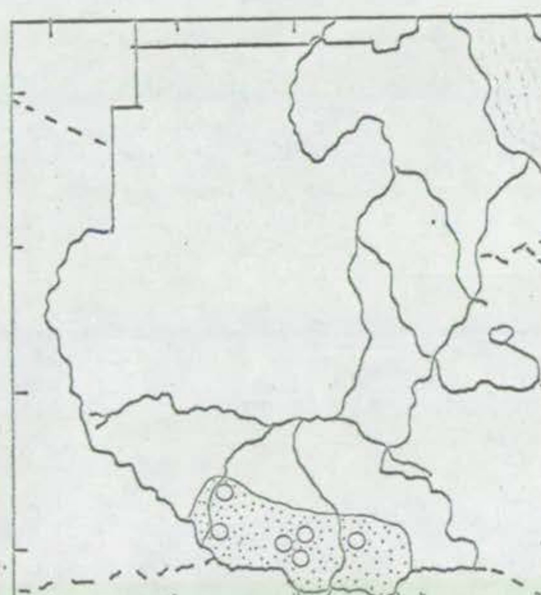
35. A. POLYACANTHA SUBSP. CAMPYLACANTHA



36. A. PERSICI FLORA

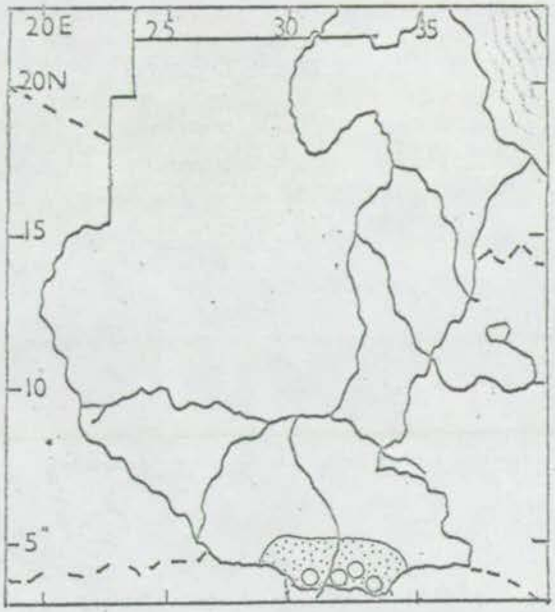


37. A. HECATOPHYLLA

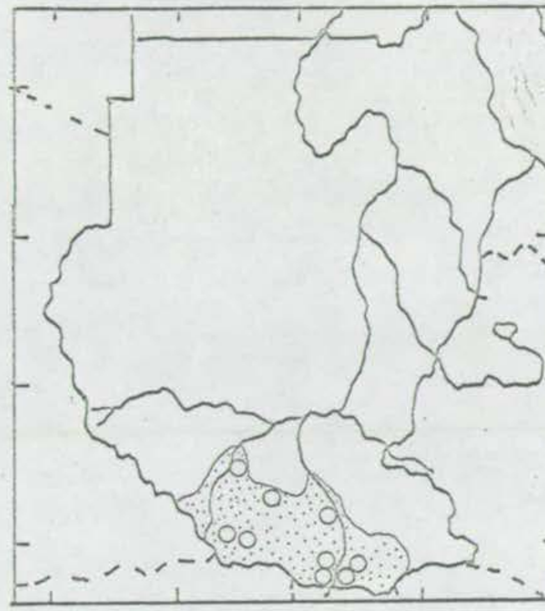


38. A.MACROSTACHYA

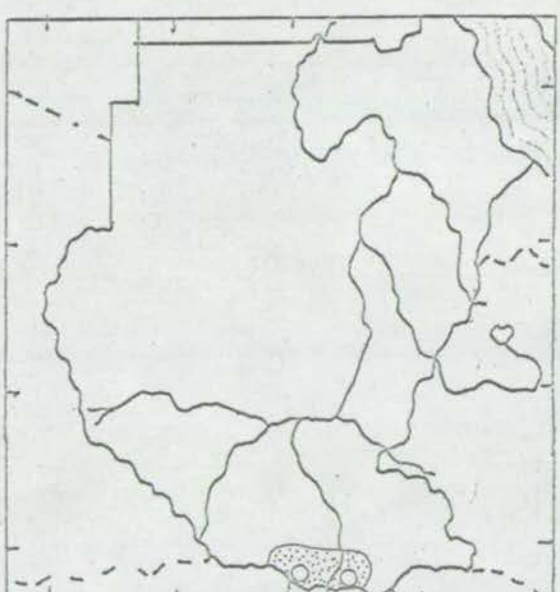
SCALE : 500 KILOMETRES.



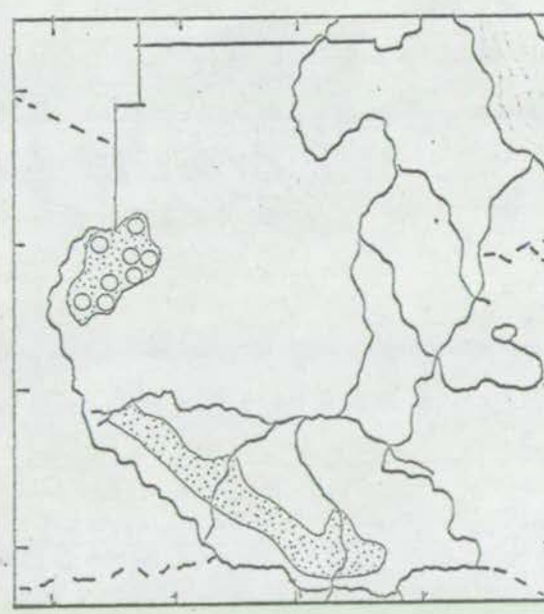
39. A. BREVISPICA



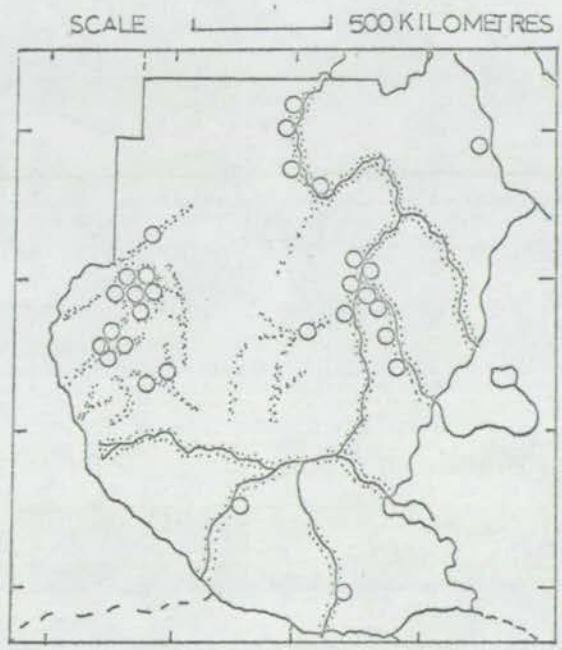
40 A SCHWEINFURTHII



41. A .PENTAGONA



42.A. ATAXACANTHA



43. A. ALBIDA

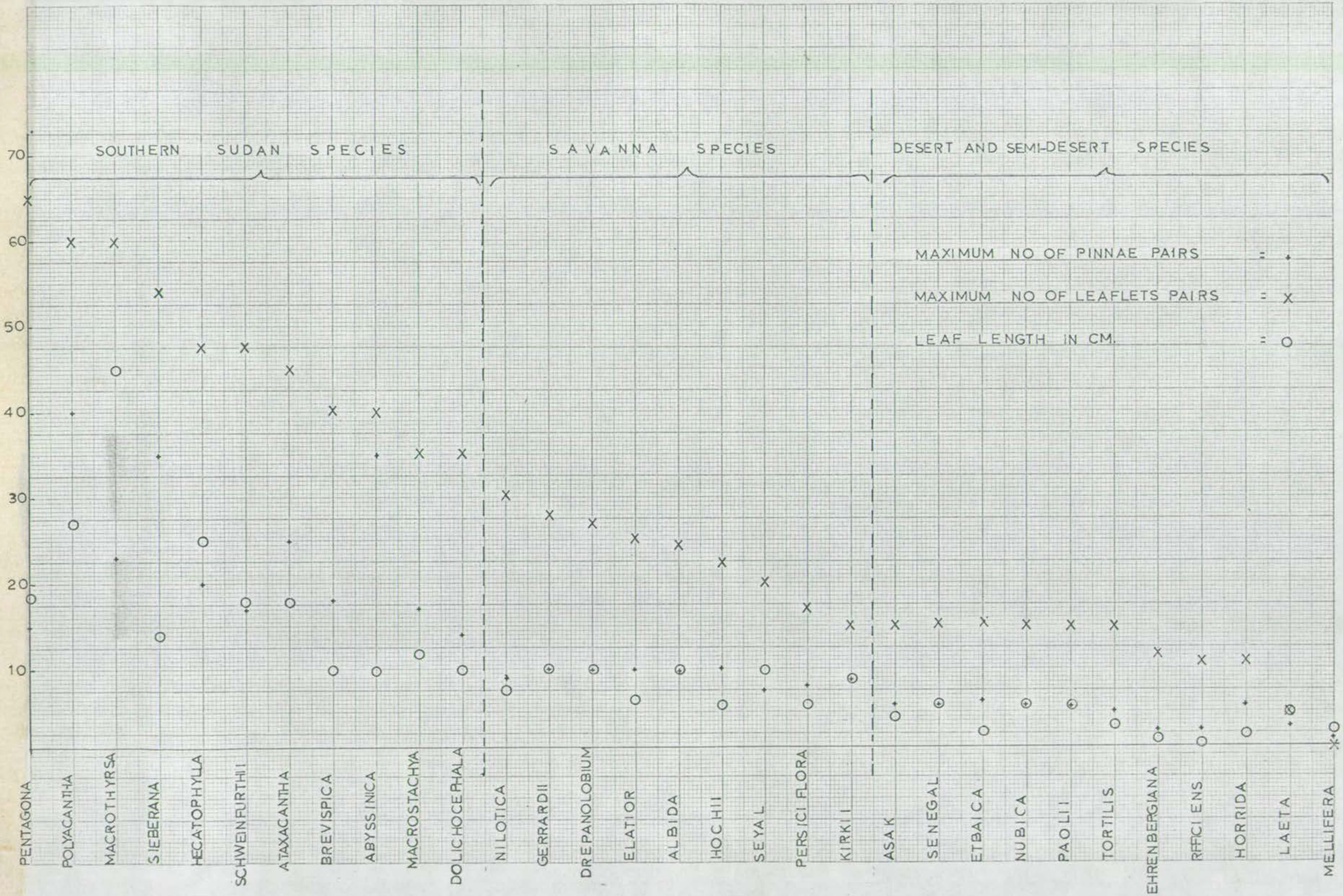
in Central and Northern Sudan, never cross the Nile westwards and must be considered as being very exact in their habitat requirements.

Morpho-ecological correlations

The correlation between ecological factors and the morphological characters is very evident in the Sudan Acacias. The only available work on this aspect is a small paper by Bond (1919); he pointed out that species occurring under arid conditions have spreading shallow roots, whereas those under favourable water conditions have deep roots.

In this study it was noticed that species in the Central and Northern Sudan living in arid or semi-arid conditions have xeromorphic characters, whereas those in the Southern Sudan with high rainfall have mesomorphic characters.

A special study was carried out to assess the morphological correlation of leaf characters of the Sudan Acacias with the three ecological zones - Northern, Central and Southern. The leaf parts of all the Acacia species were measured and the results were graphed for leaf length and the maximum number of pinnae and leaflets pairs in the three ecological zones (see Graph No. 1 page 223). The results show long leaves, high number of pinnae and leaflets in the species which occupy Southern Sudan, intermediate status in species of Central Sudan, and smallest status in species of Northern Sudan. The graph also shows that at the border lines of the three zones the species on both sides are related in leaf characters and indicate also that some species cross their borders to the adjacent zone. A. paolii, A. reficiens, A. mellifera, A. laeta and A. senegal have the smallest dimensions like those of the desert species of Northern Sudan and these are the species which


SOUTHERN SUDAN SPECIES
SAVANNA SPECIES
DESERT AND SEMI-DESERT SPECIES
MAXIMUM NO OF PINNAE PAIRS =
MAXIMUM NO OF LEAFLETS PAIRS = X
LEAF LENGTH IN CM. = O
70
60
50
40
30
20
10
PENTAGONA
POLYACANTHA
MACROTHYRSA
SIEBERANA
HECATOPHYLLA
SCHWEINFURTHII
ATAXACANTHA
BREVISPICA
ABYSSINICA
MACROSTACHYA
DOLICHOCEPHALA
NILOTICA
GERRARDII
DREPANOLOBIUM
ELATIOR
ALBIDA
HOCHII
SEYAL
PERSICIFLORA
KIRKII
ASAK
SENEGAL
ETBAICA
NUBICA
PAOLII
TORTILIS
EHRENBERGIANA
REFICIENS
HORRIDA
LAETA
MELLIFERA

usually cross their borders to the adjacent zone.

A. persiciflora from Southern Sudan appears in the graph as having smaller dimensions than expected, but this may be due to the presence of only one specimen for study. Otherwise the correlation between ecological habitats and leaf characters in the other species is perfect.

However, there are many other characters where these morpho-ecological correlations are evident, such as habit, form, bark, prickles and spines, stipules, leaves, inflorescences, flowers, pods and seeds; these characters were discussed in Chapter II. Attributes in other fields in this study (Chapter II) also revealed a strong correlation of characters with habitat (see Table No. 7 page 226).

To summarise this discussion: there is a gradual change of characters of the Acacias from the high rainfall areas in Southern Sudan to dry arid areas of Central and Northern Sudan, or from Groups II and III to Group I characters. A modification to this trend is the presence of riverine species which have less xeromorphic characters because of adaptation to favourable water conditions.

The concentration of diploid Acacias in the Southern and Central Sudan and polyploids in the Northern Sudan provides strong evidence of genetic adaptation to arid conditions. It was noticed in the field that there is a gradual creep of dry conditions from north to south causing the recession of the broad leaved forests southwards and the replacement with the Acacia savanna type of vegetation.

The genus has a tropical and subtropical distribution in the world. The number of species in the genus is about 1,000; 616 species are endemic to Australia and the rest to Africa, Central and South America and a few to Asia. Bentham (1874) believed that the Vulgares members (Groups II and III) are the ancestral type growing in tropical rain forests in South America and Africa; he thought that from these tropical centres the genus had spread southwards and northwards, and that is why it is absent in places like New Zealand. This statement to some extent agrees with my statement about the centre of diversity of the genus in the Sudan.

The successful development of the genus in the arid parts of Australia also supports my view on the favourable conditions in arid or subarid regions for the Acacias, as was seen in Central and Northern Sudan. For unknown reasons the polyploid Acacias are absent in Australia. Also members of Groups II and III (Bentham's Vulgares) are completely absent in Australia.

TABLE NO. 7 DIAGRAMMATIC TABLE SHOWING THE MORPHO-ECOLOGICAL CORRELATI[ON] IN THE STUDIED CHARACTERS OF THE SUDAN ACACIAS.

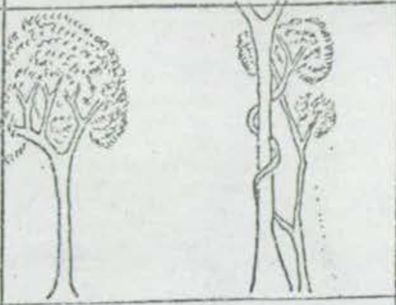
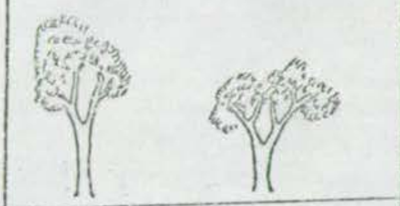
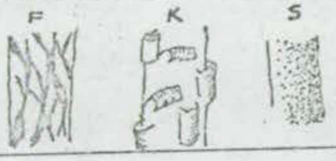
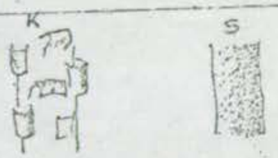
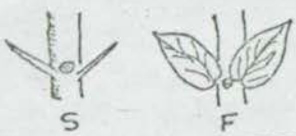
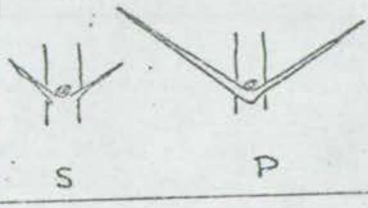
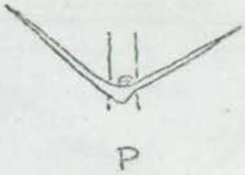
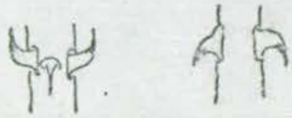
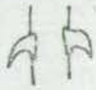
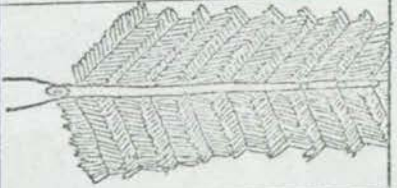
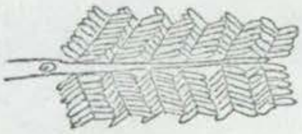
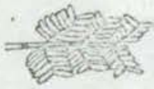
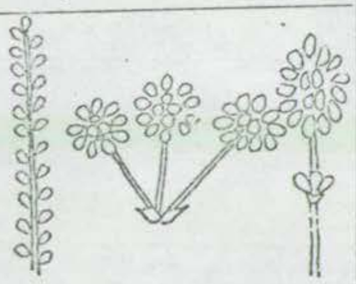
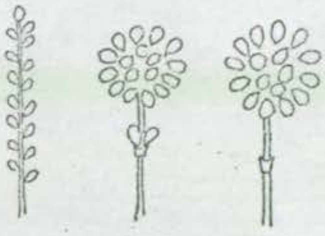
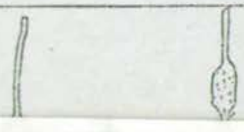
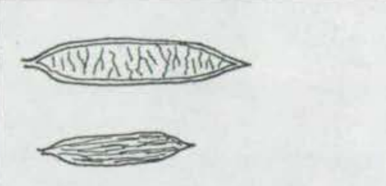
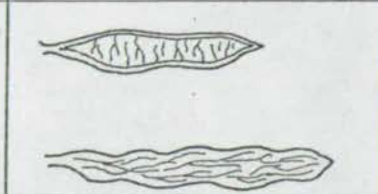
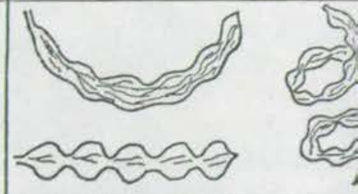
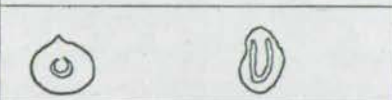
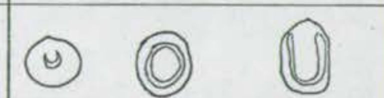
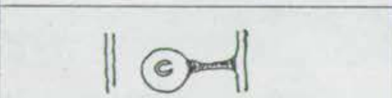
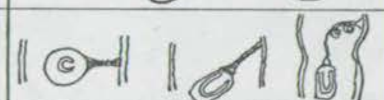
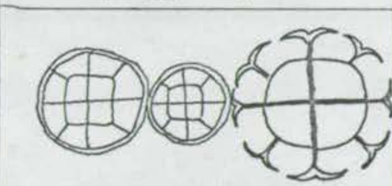
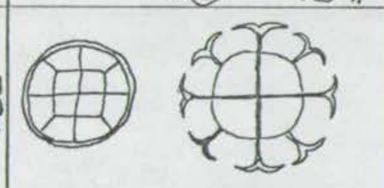
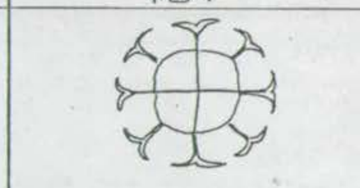
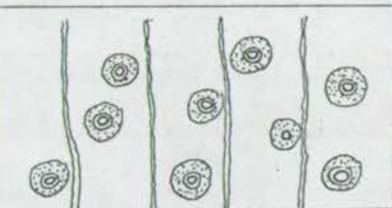
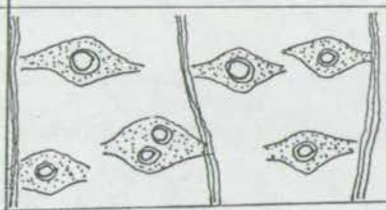
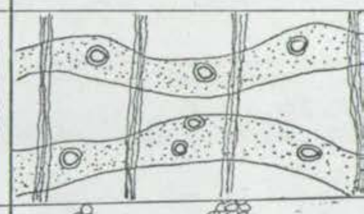
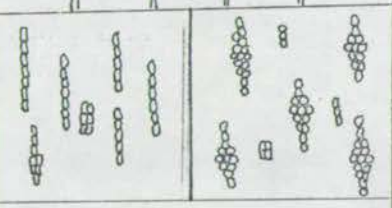
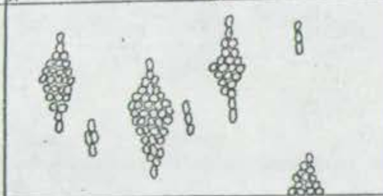
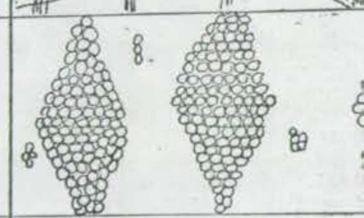
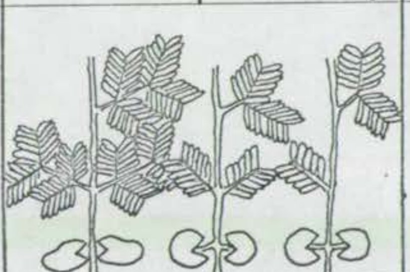
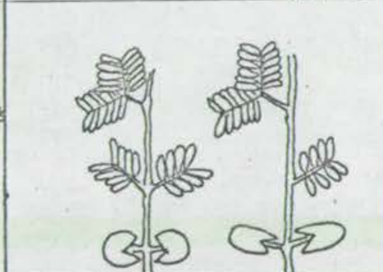
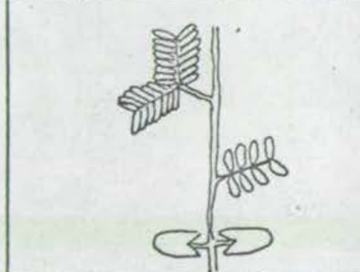
CHARACTER	SOUTHERN SUDAN	CENTRAL (+TOBOSA) SUDAN	NORTHERN SUDAN
Habit and form			
Bark Fissured (=F) Flaky (=K) Smooth (=S)			
Stipules Scale-like (=S) Foliate (=F) Spinescent (=P)			
Prickle types			
Spine sizes			
Leaf sizes			
Inflorescence types			
Ovary stipes (Gynophores)			

TABLE No. 7 (cont.)

CHARACTER	SOUTHERN SUDAN	CENTRAL(+TOBOSA) SUDAN	NORTHERN SUDAN
Perianth parts K = Calyx C = Corolla	K AND C = 5 lobes	K AND C = 4-7 lobes	K AND C = 4-7 lobes
Pod shapes			
Seed and areole shapes			
Seed position inside pod			
Pollen types			
Chromosome number	2n= 26	2n= 26 ,52	2n=52 ,104
Timber anatomy: T.S. Parenchyma Fibres Vessels (Pores) Rays			
Rays : L.S.			
Seedling development			

5. A. LAETA, CONSIDERED AS A SPECIES OF HYBRID ORIGIN

A. laeta has many characters in common with two other species with which it is usually associated in the field; these two species are A. mellifera and/or A. senegal. Aubreville (1950) observed the close affinities between A. laeta and A. senegal in habit, habitat, prickles, inflorescence and pod characters and suggested that A. laeta is a hybrid of A. senegal and another species. Jackson and Peake (1955) maintained that it is a natural hybrid between A. senegal and A. mellifera. Brenan (1959) suggested that A. laeta is a hybrid of A. mellifera and some other Acacia, most probably A. goetzei. The latter species does not occur in the Sudan. Recent workers treat A. laeta as a separate species widely distributed in Africa.

In the Sudan, A. laeta exists on heavy clay soils with A. mellifera, on light sandy soils with A. senegal, on clay soils associated with both of them, or occasionally alone. It is fertile in all areas of its distribution in Central Sudan. The three species have similar characters of habit, prickles, inflorescence, pod and seed. However, A. laeta is more closely related to A. mellifera than to A. senegal, especially its leaf characters.

A population study of the three species was carried out from ten habitats in the Sudan. 33 morphological characters were studied in the three species; a summary of the results is shown in Table No.8 page 231.

Analysis of data

Taking 33 characters and comparing them in the three species, the following points were apparent :

10 characters are similar in all 3 species,

11 characters are intermediate in A. laeta between A. mellifera and A. senegal,

9 characters are shared by A. mellifera and A. laeta,

3 characters are shared by A. senegal and A. laeta.

In the field A. senegal is easily separable from the other two species by its irregular crown and yellow-brownish bark, 3-prickled branches, and usually one or occasionally two main stems, unlike the other two which have grey bark, 2-prickled branches and many stems. Occasionally a few prickles occur on the rachis of A. laeta and A. senegal, but not A. mellifera.

The leaf gives the only character by which these three species can easily be separated, especially the number of pinnae and leaflets pairs. A. mellifera has 2 pinnae pairs; A. laeta has 3 pinnae pairs, rarely two; A. senegal has 3-4 pinnae pairs. There is always one pair of leaflets in A. mellifera; A. laeta has 1, 2, 3, 4, 5 pairs of leaflets, but 3 is most frequent; A. senegal has 8-17 pairs with an average of 12 pairs. The leaflet shapes and sizes, as seen in the Table 8, are also distinguishing features of the three species. The other relationships are clearly shown in the Table.

Scatter diagrams

Graphic presentation of some of the characters of the three species were drawn to study the position of A. laeta and its relationships with the other two species. Quantitative characters were chosen for study from the leaves and inflorescences as follows:

Scatter diagram No. 1: Shows the relationship of the number of pinnae pairs (vertical) and number of leaflets pairs (horizontal) in the three species for 10 populations selected from different localities. The results show the intermediate position of A. laeta between the other two species; as is evident from the diagonal hybrid line, A. laeta and A. mellifera were shown in the diagram to be very closely related as compared with its relationship with A. senegal.

Scatter diagram No. 2: Shows the relationship of inflorescence length (vertical) and number of leaflet pairs (horizontal) in the three species for 10 populations. The diagram shows a slight divergence from the intermediate position of A. laeta as regards the studied two characters, and again its close affinity with A. mellifera.

Scatter diagram No. 3: Shows the relationship of inflorescence length (vertical) and leaf width (horizontal) of the three species for 10 populations, and again the intermediate position of A. laeta and its affinity with A. mellifera is evident.

The results drawn from the three scatter diagrams confirm the intermediate position of A. laeta between the two other species, though it is more closely related to A. mellifera than A. senegal.

Cytologically, both A. mellifera and A. senegal are diploid 2n = 26; A. laeta is a triploid 2n = 39.

The pollen grains in A. mellifera and A. senegal have similar features like the typical pollen Type 2 of Group II, but the grains of A. laeta are slightly different in having an 18-20 celled polyad compared with the normal 16-celled polyad of the other two, and also in A. laeta the monads are slightly irregular and distorted.

Anatomically they have similar features. The seedling development of

TABLE NO. 8 SUMMARY OF MORPHOLOGICAL CHARACTERS OF A. LAETA, A. MELLIFERA AND A. SENEGAL

		A. mellifera	A. laeta	A. senegal
Habit	:	Shrub or small tree (1)-6-(9) m	Shrub or small tree 6 m	Small tree 12 m
Form	:	Round crown	Round crown	Flat or irregular
Habitat	:	Clay plains 400-600 mm R.F.	Clay plains 400-600 mm R.F. x	Sandy and clay plains 400-600 mm R.F.
Association	:	Pure or associated with the other 2 sp.	Pure or associated with the other 2 sp.	Pure or associated with the other 2 sp.
Stems	:	Many stems	Many stems	1 or 2 stems
Stem bark	:	Dark grey	Dark grey	Grey or yellow-brownish
Young branchlet	:	Glabrous to pubescent	Glabrous	Glabrous
Prickles	:	Not spinescent - in twos	Not spinescent - in twos	Not spinescent - in threes
Prickles, L, C	:	Short, dark brown, curved	Short, dark brown, curved	Short, dark brown, curved
Leaves length	:	1.6-4 cm	2.7-5.2 cm	1.1-5.3 cm
Petiole length	:	0.8-2.5 cm	0.8-2.5 cm	0.4-1.7 cm
Rachis length	:	0.5-1.7 cm	1.7-2.9 cm	0.7-3.9 cm
No. pinnae pairs	:	2 rarely 3	3 rarely 2	3 and 4
Rachillae length	:	0.2-0.8 cm	0.8-3.2 cm	1-3 cm
No. leaflet pairs	:	1	(1-2)-3-(4-5)	(8)-11-15-(17)
Leaflet length	:	0.8-1.9 cm	10.5-16 mm	3-6.5 mm
Leaflet width	:	0.4-1.4 cm	4-9 mm	0.8-2 mm
Prickles on rachis	:	Not present	Prickles may occur on rachis	Prickles may occur on rachis
Leaflet shape	:	Obovate	Obovate, oblong lanceolate	Oblong lanceolate
" indumentum	:	Glabrous	Glabrous	Pubescent
Inflorescence	:	Spicate, cream, 2-4.5 cm long	Spicate, cream, 4.5-6.2 cm	Spicate, cream, 6-10 cm long
Peduncle	:	1-1.4 cm	0.5-2 cm	0.8-1.3 cm
Flowers	:	Pedicellate 0.5-1.8 mm, K, C cream to pink	Pedicellate 0.5-1 mm, K, C cream to pink	Sessile, K, C cream to pink
K, C, A	:	K=6-1 mm, C=2.5-3.5 mm, A=7-8 mm	K=1.5x1 mm, C= 4x1 mm, A=7-8 mm	K=2x0.7 mm, C=2.5x0.3, A=4.5-5 mm
Ovary	:	Ov.= 1.5 mm, style = 7 mm, stipe = 1 mm	Ov.= 1 mm, style = 9 mm, stipe = 0.1-0.2 mm	Ov.= 0.7 mm, style = 4.5 mm, stipe 0.2 mm
Pod	:	Straw to light brown = 6.6-9 x 1.7-2.2 cm	Straw to light brown = 5.5-9 x 2-2.4 cm	Straw to light brown = 5.7-10 x 1.2-2.4 cm
" indumentum	:	Glabrous	Glabrous to pubescent	Pubescent
Seeds	:	Circular, light brown, glabrous	Circular, light brown, glabrous	Circular, light brown, glabrous
Areole	:	Crescent-like, central, open	Crescent-like, central, open	Crescent-like, central, open
Funicle	:	7-8.5 mm	8.5 mm	7.5 mm

A. laeta is the same as A. mellifera, i.e. pattern 2; it is different from that of A. senegal which has pattern 1.

Summary and discussion of A. laeta position

A. laeta is in the same Group II of the non-spinescent stipuled Acacias and shares many of the group characters as well as differing in a few others. There is a possibility of its hybrid origin as evident from the morphological characters already mentioned. The striking similarity of characters with A. mellifera makes it difficult sometimes to separate in the field unless a close look at the number of the pinnae and leaflet pairs is made. Its relationship with A. senegal is not very close and they are easily distinguished in the field.

The triploid number of its chromosomes, $2n = 39$, is a good indication of its hybrid origin. Though it is fertile and occupies wide areas and behaves as a separate species, there are certain characters which are not stable, e.g. the leaf parts number and arrangement (see fig.13 page 235) which I have found in my studied specimens. The leaflet shape is also not definite as it can be obovate or lanceolate or intermediate between both shapes. This instability of characters is evident in many other attributes of A. laeta.

Brenan (1959) suggested that it is a hybrid of A. mellifera and other species, amongst which is A. goetzei, but because the latter species itself has most unstable characters and even could be a hybrid itself (Ross. Pers. Comm), I exclude it as a possible parent.

Khan M. I. (1951) studied some Acacia hybrids and noticed a natural hybrid between A. mellifera and A. senegal; this hybrid is a triploid, fertile and has intermediate characters between the two parents. So the possibility of producing alltriploid from two parent diploids is not impossible in the Acacias.

The question of the fertility of A. laeta is difficult to answer. Triploids are usually sterile and very rare, A. laeta with 2n = 39 provides certain difficulties in pairing in meiosis. Thus the question of its fertility cannot be answered until the process of meiosis is fully investigated on fresh materials. The following are suggestions for the formation of the triploid, A. laeta:

1. It is possible that the triploid of A. laeta is formed through the two suggested diploid parents. The triploid number could have resulted by the formation of a bivalent complement from one parent and a monovalent complement from the other parent, i.e. no reduction during meiosis has taken place in one parent's complement (a situation analogous to that found on the Rosa canina complex). The resulting hybrid would be expected to be sexually infertile because of pairing difficulties during meiosis. On viewing the results produced by Khan (1951) and the present A. laeta which is fertile, it is probable that this triploid might be reproducing apomictically through agamospermy; the irregular and rather distorted pollen of A. laeta might add support to this probability. Apomictic progeny is usually uniform in characters, which is not the case with A. laeta which proved to have some unusually variable characters.
2. A. laeta could have resulted from the hybridization of a tetraploid and a diploid. The tetraploid could be a form of A. mellifera which I have not seen, or else could be another tetraploid like A. nubica, a species which is also found with A. mellifera in clay plains.
3. Newman (1934) dealing with the chromosomes of A. baileyana, an Australian

species, suggested that $n = 13$ gametic chromosome number was derived from a lower haploid number of $n = 7$, i.e. $2n = 14$, followed by the loss of one chromosome. If this assumption is correct, then $n = 13$ is a secondary basic chromosome number and the supposed 'diploid' ($2n = 26$) is really a tetraploid. Accordingly the present triploid (A. laeta) would be a hexaploid which might allow some degree of fertility.

In conclusion, it is quite possible that A. laeta is of hybrid origin from A. mellifera and A. senegal and that the closer affinity with A. mellifera is probably due to back crossing with it in the past. It has now established itself as a separate species which reproduces by seeds, and has occupied vast areas in the Sudan and other African countries. The instability in number and arrangement of its leaf parts is not unexpected with a taxon of hybrid origin. By what means a species with 39 manages to be fertile must await detailed cytological investigation.

A.LAETA: NUMBER AND ARRANGEMENT OF LEAF PARTS.

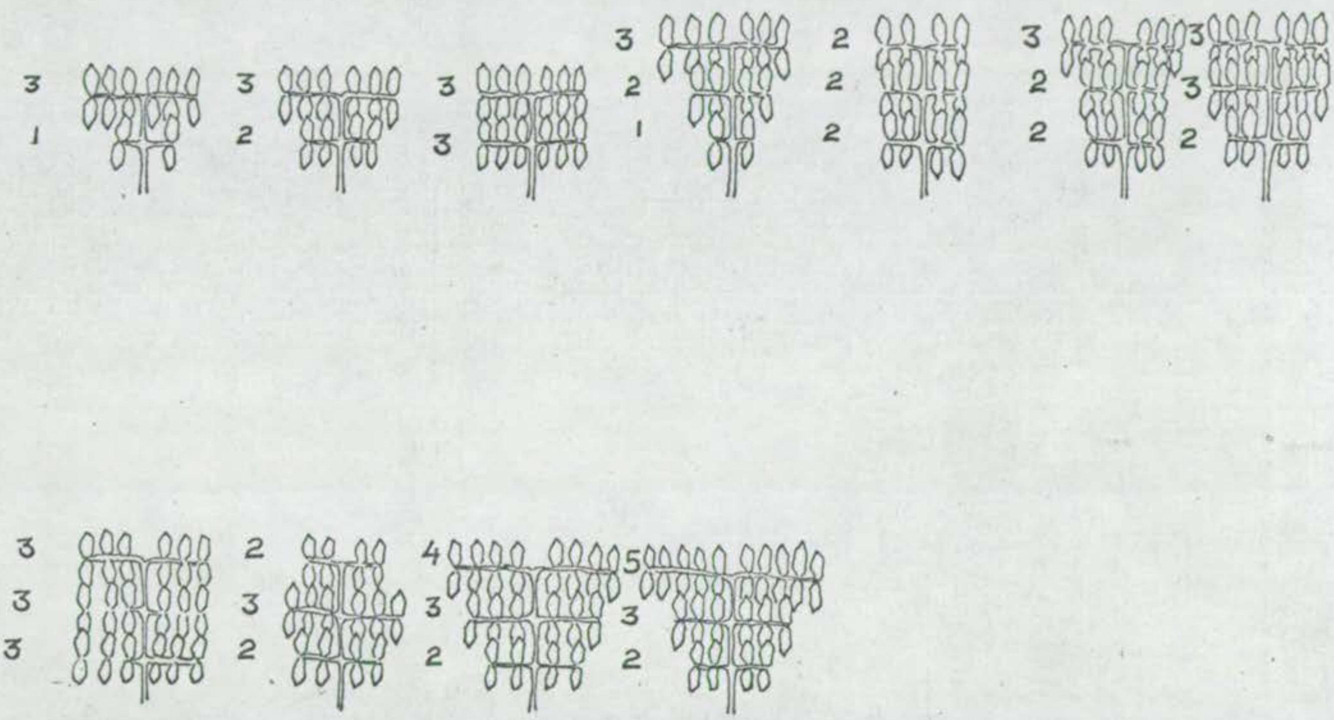
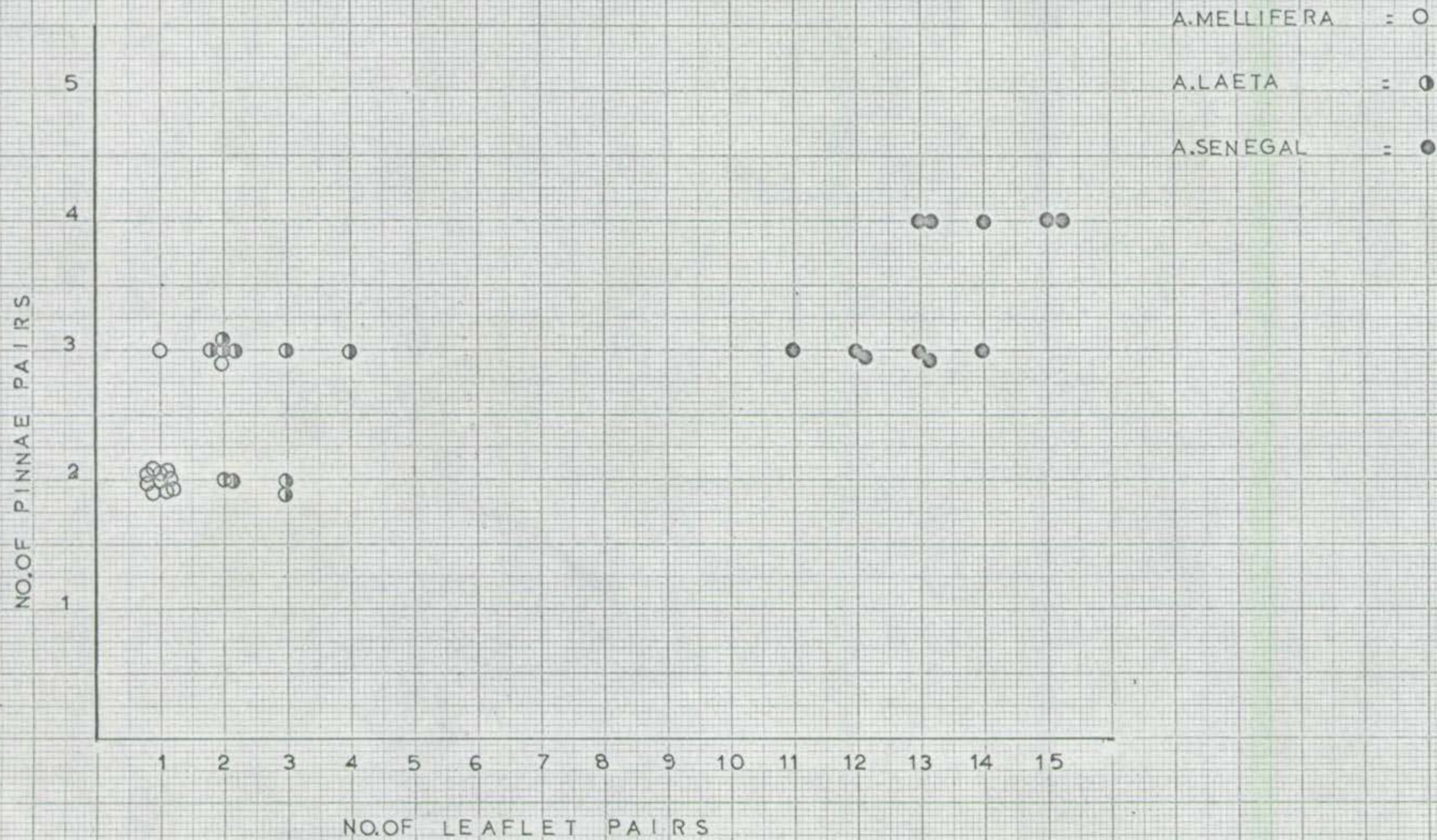
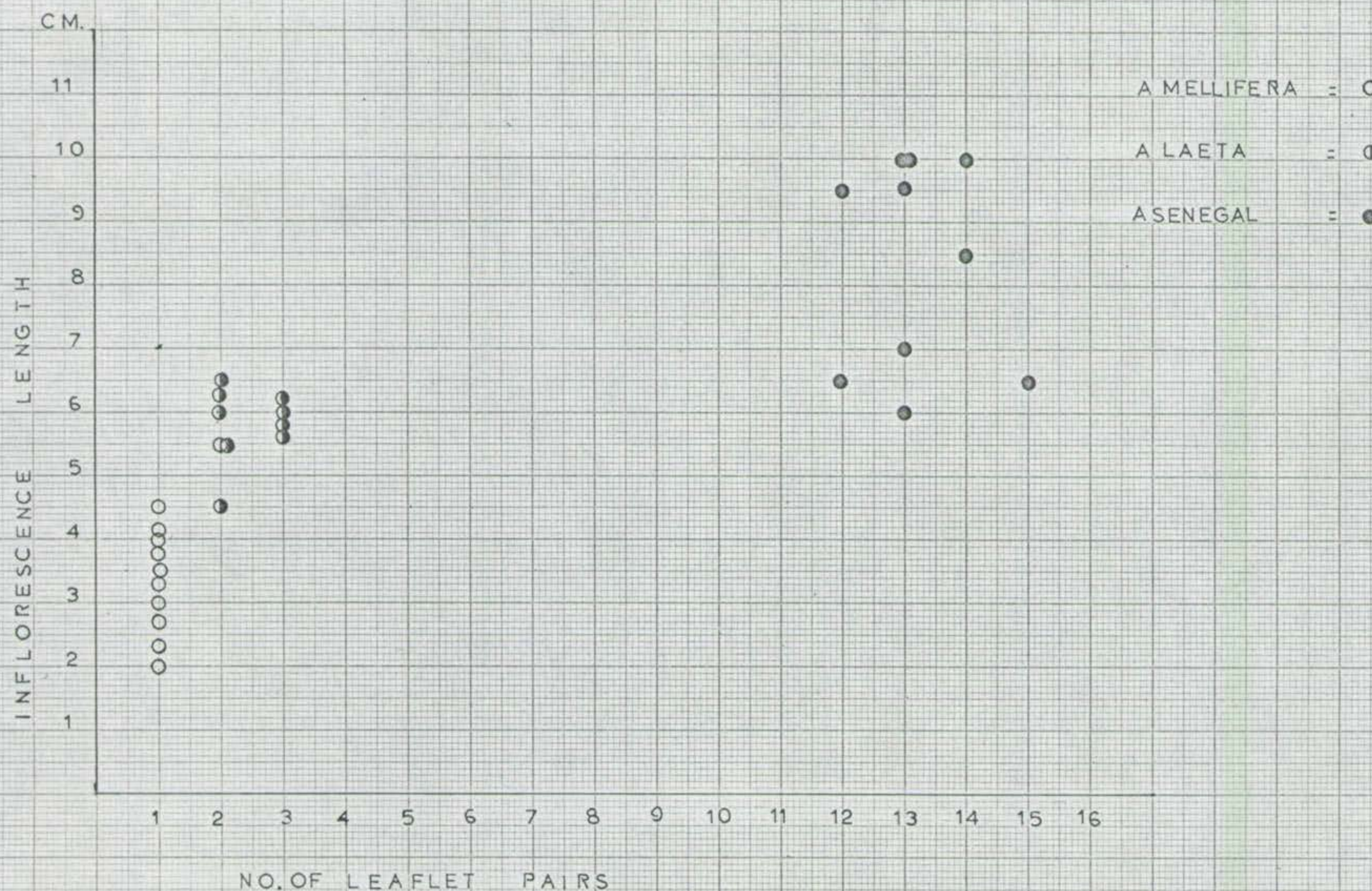


FIG .13 A.laeta,leaf parts.

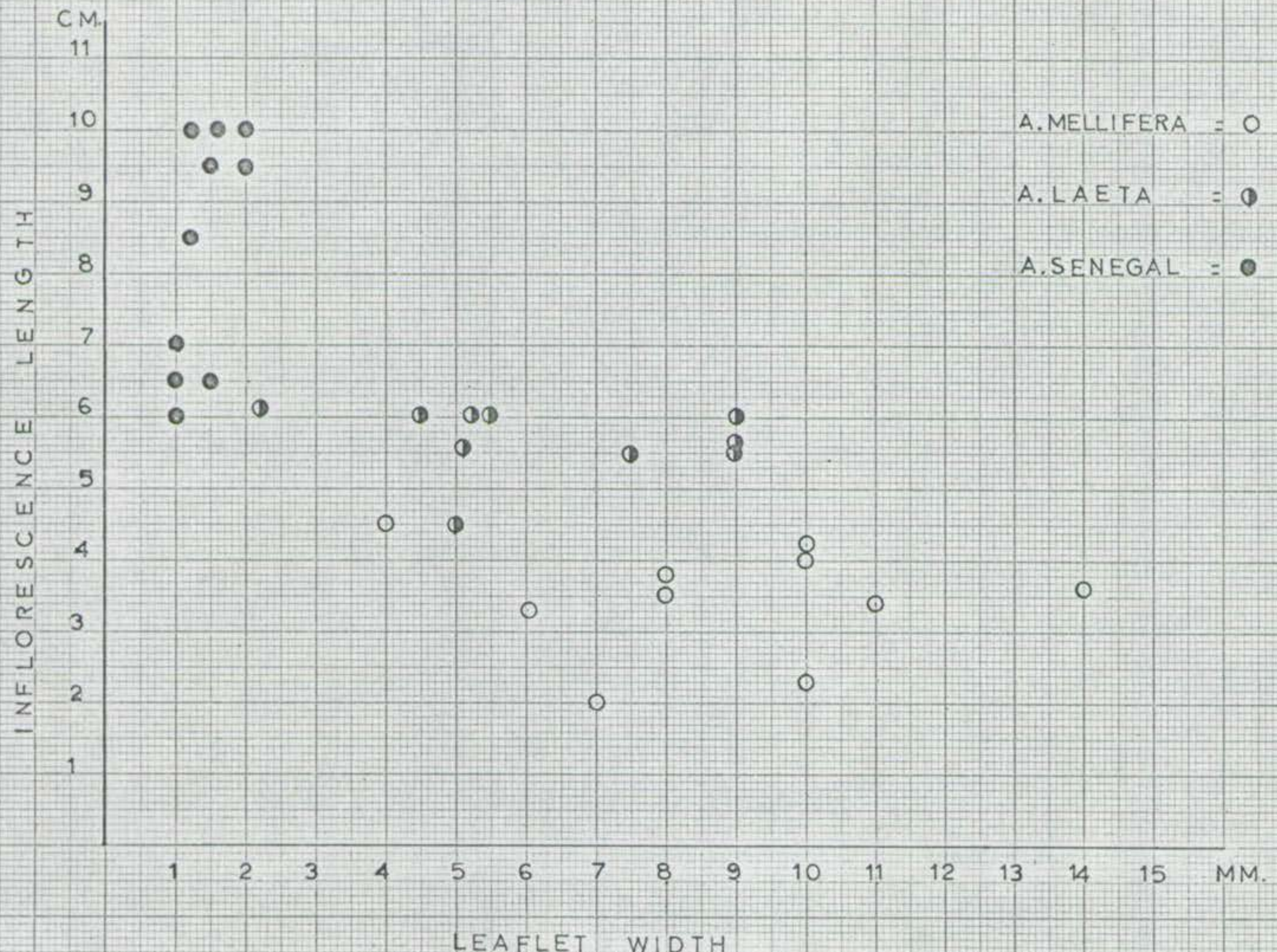
Scatter diagram 1. Relatinship of number of pinnae pairs and of leaflets pairs of A. laeta A.mellifera and A.senegal



Scatter diagram 2. Relationship of inflorescence length and number of leaflet pairs in A.laeta, A.mellifera and A.senegal.



Scatter diagram 3. Relationship of inflorescence length and leaflet width in A. laeta, A. mellifera and A. senegal



6. STUDY OF A. ALBIDA IN RELATION TO OTHER ACACIAS

A. albida is worthy of special treatment in this study because of its many anomalous characters as compared with the other Acacias, and also because some French botanists have treated it as a separate genus, Faidherbia. In this study it has been treated as an Acacia species, but put in a separate group to emphasize its anomalous position within the genus.

Past taxonomic work on A. albida

The species was firstly described by Delile in Fl. Aegypt: 142, t. 52, fig. 3 (1813). Type: Egypt, Philae, Nectoux (M.P.U., holotype). The synonyms are many and have been dealt with by Ross (1966).

Baillon (1863) was the first to draw attention to some anomalous characters of A. albida, but kept it within the Acacias. Bentham (1875) placed it with A. horrida and A. lahai together in the Gerontogeae, belonging to the series Gummiferae; he based this on the stipule and inflorescence characters.

Chevalier (1934) was convinced, because of the many anomalies of A. albida, that it was sufficiently different from other Acacias, and consequently proposed a monotypic genus, Faidherbia, intermediate between the Acacias and the Ingeae tribe, to accommodate it. Only a few French botanists adopted the new name, Faidherbia albida (Del.) A. Chev., the majority of the subsequent workers continuing to use the old name, A. albida. Chevalier's decision was based mainly on morphological and timber characters; he noticed the uni and biseriate rays of its timber as compared with the multiseriate rays of A. nilotica. In my study uni and biseriate rays have been found in all the climbers (Group III).

Brenan (1959) pointed out some morphological anomalies, treated the species as A. albida and created two races based on the indumentum of the different parts of the plant.

Wickens (1967, 1969), after studying A. albida in Western Sudan, wrote two papers on its ecology and taxonomy; he summarised the taxonomic treatment of the species and stated: "I have been unable to suggest any other species within the genus with which it might be allied and there is a steadily mounting accumulation of evidence pointing to the anomalous position of A. albida within the infra-generic classification". He stressed the fact that more work is needed to study Acacia species and related genera before coming to a definite conclusion about A. albida. At the same time Cutler (1969) made detailed anatomical studies of the vegetative parts and concluded that A. albida belongs anatomically to the group of species in the genus with narrow rays (i.e. my Group III).

Guinet (1969) made a detailed palynological study of the Mimosaceae, and on the basis of the different characters of A. albida pollen and its strong connate stamens, decided to keep it out of the Acacias and retained the genus Faidherbia in the Ingeae tribe.

Robbertse and Schijff (1971) wrote a paper on the genus Acacia in South Africa and put A. albida with some of the climbers in one group called 'sub-order Farinosae', based on the similarity of having bipinnate leaves appearing after the cotyledons in the seedlings.

Halvey (1971) made a study of A. albida in Palestine and mentioned its distribution in the Mediterranean parts of that country. He also stated that the chromosome number is 2n = 26 in Africa and 2n = 52 in Palestine, a difference presumably associated with its northern extension.

In this paper micro- and macromorphological characters of A. albida were studied from the Sudan specimens and compared with the available morphological data on the species. The species is also studied here anatomically, palynologically and cytologically, as well as investigating the seedling ontogeny of the Sudan Acacias. On the bases of these studies A. albida is compared with characters of the genus as a whole, and its relationship with the infrageneric classification.

Anomalies of A. albida

The general description of A. albida is mentioned on page 239. It suffices to mention here those characters in which it differs from the other Acacias:

a) Gross morphology

Habit:	Leaves shed in the rainy season and retained in the dry season. The largest Acacia tree.
Branches:	Young twigs milky white.
Leaves:	Petioles eglandular; glandular between the pinnae and leaflet pairs.
Flower:	Anthers eglandular and longer than in other Acacias, stamen filaments connate above the ovary level; *anther sacs larger than other Acacias.
Pod:	Orange, pulpy. *Venation usually not apparent.
Seedling:	Cotyledons obovate and sessile; first leaf bipinnate *with one pair of pinnae, together with spinescent stipule in the seedling stage.

b) Anatomy

*Transition from root to stem tissues delayed until just below the cotyledons.

*Outline of hypocotyl undulate.

*Rays in the timber uni- and biseriate, semi-storied.

*Parenchyma and fibrous tissues semi-storied.

c) Palynology

*Polyad largest in size.

26-32 monads in the polyad.

4 pores, no fissures.

(Characters preceded by an asterisk are data collected in this study).

Affinities of A. albida with other Acacias (See Table No. 9 page 243).

A. albida, having spinescent stipules, is related to Group I but differs generally in the characters which separates it from other Acacias. Its floral characters are nearer to Group III in having a long stipe (gynophore) which is pubescent, and in having stamens connate as in Groups II and III. The size of the anther sac in A. albida is larger than in other Acacias and decreases from Group I to Group III. The pod characters, which are unique in A. albida, come nearer Group I than to other groups as regards shape, which varies from falcate to spiral; the pod is not compressed as in the members of Group I. The seeds and the areole characters are related to those of Group I in having U or O-shaped areoles. Anatomically its timber characters are related to Group III in having uni- and biseriate rays, but nearer to Group I in the abundance of parenchyma tissues. The pollen characters, though different from other Acacias, are nearer to Groups

TABLE NO 9 COMPARISON OF A. ALBIDA (GROUP IV) WITH OTHER ACACIA GROUPS

Character	A. albida Group IV	Group I	Group II	Group III
Shedding of leaves	In rainy season	In dry season	In dry season	In dry season
Colour of young branches	Milky white	Grey, brown, pink	Grey, brown, pink	Grey, brown, pink
Stipules	Spinescent	Spinescent	Non-spinescent	Non-spinescent
Glands on petioles	Eglandular	Glandular	Glandular	Glandular
Glands on rachis	In between pinnae and leaflets pairs	Spread along the rachis	Spread along the rachis	Spread along the rachis
Inflorescence type	Spicate	Spicate & capitate	Spicate	Spicate & capitate
Anthers	Eglandular & united at the base	Glandular, free	Glandular, united at the base	Glandular, united at the base
Size of anther sac	Largest	Large	Small	Smallest
Pod: colour	Orange	Grey, brown, yellow	Brown	Brown
venation	Absent	Longitudinal	Horizontal	Horizontal
Seed: shape	Obovate	Oblong	Orbicular	Orbicular to obovate
areole	U-shape or closed 0	U-shaped or closed 0	Crescent	Crescent to U-shaped
1st leaf in the seedling	Bipinnate - one pair	Pinnate	Pinnate	Bipinnate - 2 pairs
Seedling stipules	Spinescent	Spinescent	Hyaline (scale-like)	Foliate
Transition of root-stem	Just before the cotyledons	1 mm above hypocotyl base	1 mm above hypocotyl base	1 mm above hypocotyl base
Timber anatomy : rays	Uni & biseriate rays	Uni, bi & multiseriate	Uni, bi & multiseriate	Uni & biseriate
Pollen grains : polyad	26-32 monads	16 monads	16 monads	16 monads
Pollen pores	4	3	3	3
" fissures	Absent	Present	Absent	Absent
No. of chromosomes 2n	26, 52	26, 52, 104	26	26

II and III in not having fissures; this character is significant because other Acacias with spinescent stipules have fissured pollen.

Conclusion

In this study this tree is considered as a spinescent Acacia, but put separately in a monotypic group to emphasize its anomalies. It is true that so far not enough is known of the characters of the genus Acacia on a world-wide basis, but with our existing knowledge of the Australian species which apparently belong to a separate evolutionary line, and from the available knowledge of the Asian and American species, A. albida definitely stands on its own among the Acacias with no definite affinities to other groups in the genus.

IV TAXONOMIC DISCUSSION

RELATIONSHIP OF GROUPS IN THIS STUDY

Acacia is a large genus (1000 spp +) showing a wide range of variation. In this study only the Sudan species were examined comprehensively; though giving a fair representation of African species this is still a tiny portion of the genus, so that it was not possible to review the whole range of variation in the genus. This work is important in producing a better understanding of the genus by the correlation of exomorphic and endomorphic characters in an attempt to arrive at a more natural classification of the Acacias. New characters were utilised here from different fields of study to add to our present knowledge, and care was taken that there was no a priori weighting of certain characters, but an overall correlation of attributes.

To give a better view of the relationship of the four suggested groups, a tabular statement is presented of the more important characters (see Table No. 10 page 246).

The most important aspect for discussion is the applicability of these four groups based on study of the Sudanese Acacias to the rest of the bipinnate Acacias and their value in suggesting the phyletic lines on which the genus has developed.

RELATIONSHIP OF THE PROPOSED GROUPS WITH OTHER AFRICAN ACACIAS

The known African species, according to the published literature, are about 110 native species. The Sudan species are 31, constituting about one-third of the total African species.

TABLE NO.10 IMPORTANT CHARACTERS OF THE ACACIA GROUPS PROPOSED

Characters	Group I	Group II	Group III	Group IV (A. albida)
Habit	Trees and shrubs	Trees and shrubs	Climbers	Trees
Armature : Spines	Present	Absent	Absent	Present
: Prickles	Absent	In pairs, few rarely scattered on internodes	Scattered on internodes and rachis	Absent
Stipules	Spinescent	Scale-like (non-spinescent)	Foliate (non-spinescent)	Spinescent
Leaves : Petiole glands	Petiole glandular	Petiole glandular	Petiole glandular	Petiole eglandular
: Rachis glands	Between pinnae pairs	Between pinnae pairs	Between pinnae pairs	At junction of pinnae pairs
Inflorescence	Globose, sub-globose and spicate	All spicate	Globose and spicate	Spicate
Involucel bract	Present	Absent	Absent (2 bracts under peduncle)	Absent
Floral bract	Present	Absent	Present	Absent
Flowers : Sex	Hermaphrodite and male flowers	Hermaphrodite flowers only	Hermaphrodite flowers only	Hermaphrodite flowers only
: Calyx and corolla lobes	4-8 lobes	5 lobes	5 lobes	5 lobes
Stamens : United or free	Free	Slightly united	United at base	United
: Anthers glands	Glandular	Glandular	Glandular	Eglandular
: Anthers width μ	Large (160-480 μ)	Small (184 μ)	Smallest (160 μ)	Largest (592 μ)
Ovary stipe (gynophore)	Sessile or very short	Short stipes	Longer than ovary	Short
: Colour	Creamy-white, yellow, orange or pink	Creamy-white or pink	Creamy-white	Creamy-white
Pods : Shape	Straight, falcate, spiral and narrow	Straight and broad	Straight and broad	Coiled and broad
: Pulpy or not	Occasionally pulpy	Not pulpy	Not pulpy	Pulpy

TABLE NO.10 (Cont.)

Characters	Group I	Group II	Group III	Group IV (A. albida)
Pods : Margin	Entire, lobed or constricted	Entire, or rarely lobed	Entire	Entire
: Compressed or not	Not compressed	Compressed	Compressed	Not compressed
: Colour	Light brown, olive-green or pink	Dark brown or yellow	Dark brown	Orange
: Venation	Longitudinal, oblique or not apparent	Horizontal	Horizontal	Longitudinal or not apparent
Seeds: Position inside pods	Lie longitudinally or obliquely	Lie horizontally	Lie horizontally	Oblique or horizontal
: Shape	Oblong	Orbicular	Orbicular to obovate	Obovate
: Areole	U or O-shaped, marginal	Crescent-shape, central	Crescent-shape, central, and U-shaped marginal	O or U-shaped, marginal
: Funicle	Long and slender	Short and broad	Short and broad	Short and broad
Seeds number	High (6-15)	Low (3-6)	Low (3-6)	High (6-15)
Seedlings development	Pattern 1 and 2	Pattern 1 and 2	Pattern 3a	Pattern 3c
Anatomy : Prickles and spines	Spines of endogenous origin	Prickles of exogenous origin	Prickles of exogenous origin	Spines of endogenous origin
: Timber parenchyma	Confluent type	Aliform to confluent types	Absent or vasicentric	Semi-storied
: Timber rays	Mainly large multi-seriate rays, few bi- and uni-seriate rays	Mainly small multi-seriate rays, few bi- and uni-seriate rays	Mainly uni-seriate rays, few bi-seriate rays	Mainly uni-seriate rays, few bi-seriate rays
: Root-stem transition	Low	Low	Low	High
Palynology : No. cells in polyad	16-celled	16-celled	16-celled	28-36-celled
: Polyad diam. μ	40-56 μ	32-36 μ	38-49 μ	110-125 μ
: Pores	3	4	4	4

TABLE NO10 (Cont.)

Characters		Group I	Group II	Group III	Group IV (A. albida)
Palynology	: Fissures	3	Absent	Absent	Absent
	: Exine outline	Broken	Continuous	Continuous	Continuous
	: Exine structure	Psilate	Smooth	Smooth	Areolate
	: Type	Type 1	Type 2a	Type 2b	A.albida type
Cytology	: 2n =	26, 52, 104 (diploid and polyploid)	26 (diploid)	26 (diploid)	26 (diploid) (Palestine 2n = 52)
Distribution of species		Mostly Northern and Central Sudan, also found in Southern Sudan	Southern and Central	Southern	All over Sudan
Ecological habitats		Desert, semi-desert, dry savanna	Savanna and high rainfall areas	High rainfall areas	Riverine

The following Table No. 11 shows the known endemic African species (excluding the Sudan Acacias) arranged within the proposed four groups:

TABLE NO. 11

Group I	Group II	Group III
Acacia zanzibarica	A. mellifera subsp. detinens	A. adenocalyx
A. ancistroclada	A. nigrescens	A. latistipulata
A. kirkii subsp. kirkii	A. erubescens	A. kamerunensis
A. xanthophloea	A. tanganyikensis	A. monticola
A. nilotica subsp. indica subsp. kraussiana subsp. leiocarpa	A. revumae	A. schweinfurthii var. sericea
	A. goetzee	A. taylorii
A. pilispina	A. circummorginata	A. kraussiana
A. etbaica subsp. uncinata subsp. australis subsp. platycarpa	A. condyloclada	A. montigena
	A. thomasii	A. lujae
A. clavigera	A. chariessa	A. ciliolata
A. lasiopetala	A. galpinii	A. pentaptera
A. pseudofistula	A. caffra	
A. bullockii	A. hereroensis	
A. erythrophloea	A. fleckii	
A. malacocephala	A. welwitschii	
A. mbuluensis	A. dulcis	
A. burttii	A. pallens	
A. arenaria		
A. fischeri		
A. sieberana var. woodii		

TABLE NO.11 (cont.)

Group I	Group II	Group III
A. stuhlmanii		
A. edgeworthii		
A. turnbulliana		
A. lahai		
A. bussei		
A. karoo		
A. davyi		
A. tenuispina		
A. exuvialis		
A. borleae		
A. torrei		
A. permixta		
A. nebrownii		
A. swazica		
A. giraffae		
A. haematoxylon		
A. rehmanniana		
A. luederitzii		
A. tortilis subsp. heterocantha		
A. rubusta		
A. grandicornuta		
A. hebeclada		
A. antunesii		

TABLE NO. 11(cont.)

Group I	Group II	Group III
A. dekandtiana		
A. tristis		
A. rogersii		
A. litakunensis		
A. hirtella		
A. natalitia		
A. gummifera		

To summarise this table quantitatively the following result emerges (here 'Africa' excludes the Sudan).

Group	Africa	Sudan	Total
I	49	18	67
II	18	8	26
III	12	4	16
IV	1	1	1
Total number of species in Africa			110

As noticed from these results, Group I has 67 species, which is the largest group in Africa as well as in the Sudan. North of the equator, due to homogenous ecological conditions, members of Group I actually occupy horizontal belts running east and west across Africa (see Aubreville 1950). South of the equator, according to the personal information I have collected from many workers, Acacias also have a wide distribution. They have succeeded in colonizing the savanna and arid zones which constitutes many parts of Africa. Groups II and III have 26 and 16 species in Africa respectively; they also seem to occupy high rainfall areas of more than 750 mm, as in the Sudan, though Group III likes tropical rain forest habitats. So the ecological correlation with the distribution of the species also holds well in Africa but not necessarily in a south to north direction as is the case in the Sudan.

Morphological characters of the African species, as published in the African literature, fit well within the proposed four groups without exception; the endomorphic characters, as apparent from this work, are correlated with certain morphological characters and similarly fit well with the proposed groups. A. albida, widely spread in Africa, has the same anomalous characters discussed in this study, and stands alone in a separate group.

Some of the Sudan Acacias from the different four groups are also represented in Asia and America in addition to the local related species. To all these the present classification is equally applied. Thus this classification covers a wide range of species in Africa, Asia and America. In Australia there are few species belonging to Group I, namely Acacia suberosa, A. bidwilli, and A. pallida; they were all put by Bentham under the Australian Gummiferae.

Going back to the African Acacias, it is noticed that there are few species in Tropical West Africa: Hutchinson & Dalzeil (1927-28) described only 17 species; G. Roberty (1948) described 12 species in his study of West African Acacias. In the Congo and Ruanda-Urundi 19 species were described, in Angola 25 species, and in the north western parts of Africa Aubreville described 19 species. Comparing these figures with East and Central Africa, the Sudan has 31 species, East Africa (Uganda, Kenya and Tanzania) 63 species, and Central Africa (Portuguese East Africa, Malawi, Zambia and Southern Rhodesia) 54 species. South Africa has less species than Central Africa, probably about 30 species. These distributional figures indicate that East Central Africa has the largest number of species and widest ranges of variation amongst the species. It can be considered as the centre of diversity of the genus in Africa.

There are, however, two species, namely A. gummifera and A. ehrenbergiana, which are endemic in the northern part of the Sahara desert and have never appeared in areas south of the equator. They have typical xeromorphic characters and could be a special speciation in that extreme arid habitat which does not exist elsewhere in Africa. A. gummifera is endemic to Morocco and A. ehrenbergiana has a continuous distribution in the northern Sahara desert.

PHYLOGENY OF THE ACACIAS

The limited number of the Acacia species studied here makes the task of a phylogenetic interpretation of this large genus a difficult one. Comprehensive information on the characters of the genus is lacking. In spite of this, some workers have endeavoured to speculate on the phylogeny of the genus, often on the basis of a few characters. In this discussion I attempt to establish certain evolutionary trends in the genus from the information collected in this work, in addition to the present literature. A hypothetical phylogenetic interpretation of the present data is also suggested for the groups studied.

SUGGESTED EVOLUTIONARY TRENDS IN THE ACACIA GROUPS STUDIED

When the overall characters of the Acacias are considered, it is evident that some parts of the plant have evolved faster and others slower or not at all.

The two major characters most discussed in the Acacias are the stipules and the inflorescence types, and there seems to be a general agreement on the fact that the spinescent stipules and the capitate inflorescences are derived from the foliate and scale-like stipules and spicate inflorescences respectively. According to this trend, Group I should be considered as relatively more advanced than Groups II and III. However, a few members of Group I, although having spinescent stipules, have retained a spicate inflorescence, e.g. A. horrida and A. lahai. Members of Group II are more homogeneous in the stipule and inflorescence characters, in that they all have non-spinescent scale-like stipules and a spicate inflorescence. Group III has capitate inflorescences (A. ataxacantha is an exception in having a spicate inflorescence) but retains foliate stipules. It thus has a status intermediate between Groups I and II in these two characters.

The appearance of male flowers, together with hermaphrodite flowers, in Group I can be interpreted as a specialised and advanced character, as compared with the other groups, where unisexual flowers are absent. Also the same Group I has evolved flowers of more elaborate colours, e.g. orange and yellow, which are absent in the other groups, and can be considered as a probable improvement in its pollination mechanism.

Two important evolutionary features occurring in Group I are the development of fissured pollen and the occurrence of polyploidy. The fissured pollen of Group I is considered by many workers, amongst them Guinet (1969), as an advanced type as compared with the non-fissured types of the other groups. There is a parallelism between plant spine characteristics and pollen features in the Acacia: stipular spines go with a high degree of differentiation in the pollen grains. Conversely, non-stipular prickles go with a low degree of pollen differentiation.

The cytological studies in this work have shown the presence of polyploidy only in Group I; polyploidy is definitely a derived condition. It can be argued that polyploidy occurs in many ancestral groups of taxa, but the fact that it occurs only in Group I is indicative of a specialised 'grade' characters, which is absent in the other groups, and it can be accepted that the polyploid Acacias are of more recent origin than the related diploid ones.

Stebbins (1952) stated that the rate of evolution appears to have been frequently speeded up by aridity; Acacia provides evidence for this view. Members of Group I, which occupy the most arid zones as compared with the other groups, have evolved many xerophytic characters, e.g. reduction in leaf surface by reducing the leaf length, number of pinnae and leaflets, and even the size of the leaflets. Again, it might be aruged that this sequence might have been reversed, or that the ancestral Acacias had xeromorphic characters. This is a debatable subject and it is difficult to ascertain any facts. But looking at the present Acacias we could see clearly this evolution towards xeromorphy apparent in Group I only.

Group IV (A. albida) seems to have evolved in a separate line and has no relatives amongst the present Acacias, and could be considered as ancient on this basis.

SUMMARY OF THE DISCUSSION

In view of the previous account of the suggested evolutionary trends of some characters of the studied Acacias, I tend to draw the following suggestions on the phyletic position of the four groups :

1. Species of Group I have more advanced characters than those of the other groups and are ecologically more adaptable. They have occupied more areas in the world, especially the unfavourable arid parts, and this has helped to speed up its rate of evolution.

2. Group II, a homogeneous group, is relatively less advanced than Group I; it is less adaptable and rather demanding in habitat and consequently less widely distributed in the Sudan and the world than Group I. This is evident in its absence from Australia.

3. Group III is very closely related to Group II. Group III are all climbers and have many more advanced characters than Group II, especially in seedling development and timber anatomy. I tend to place it in an intermediate stage of advancement between that of Groups I and II, but forming a separate phylogenetic branch.

4. A. albida (Group IV) is distinguished from the other groups by many anomalous characters. It has some characters in common with all the other groups and can be considered as a separate line of evolution, probably of ancient descent due to the absence of any existing relative in the genus.

These conclusions differ very much from those arrived at by Andrew (1914) and Atchison (1948) who both suggested that the Gummiferae (Group I) is ancestral and the Vulgares (II and III) are recent. I agree with them in putting the Australian phyllodic Acacias as the most advanced ones. I differ also from Robbertse and Schijff (1971) who suggested the ancestral group to be the 'Farinosae' which includes the capitate climbers and A. albida, a most unnatural grouping. The phylogenic conclusions arrived at by Guinet (1969), though based on the pollen characters, agree with my sequence of Vulgares (II and III), Gummiferae (Group I) and the Australian phyllodinae; I only differ from Guinet in separating the climbers from the Vulgares. Bentham has also suggested A. pennata (Group III pro parte) as a possible original form on the basis of its wide distribution. It is noticed that all these conclusions were drawn from a few characters, and more often from one character only; this might be the reason for this wide range of contradictions of the different authors.

My conclusions are specific to the Sudan Groups with a general acceptance of the Australian species as highly advanced on the basis of the characters studied here. I have used a wider range of characters in this study, so that the suggested evolutionary conclusions are consequently more justifiable than those of other botanists.

No attempt is made here to speculate on the characters of the original stock of the Acacias, but I will conclude by drawing a hypothetical phylogenetic tree which I think is applicable to the Sudan groups. (See fig. 14 page 258).

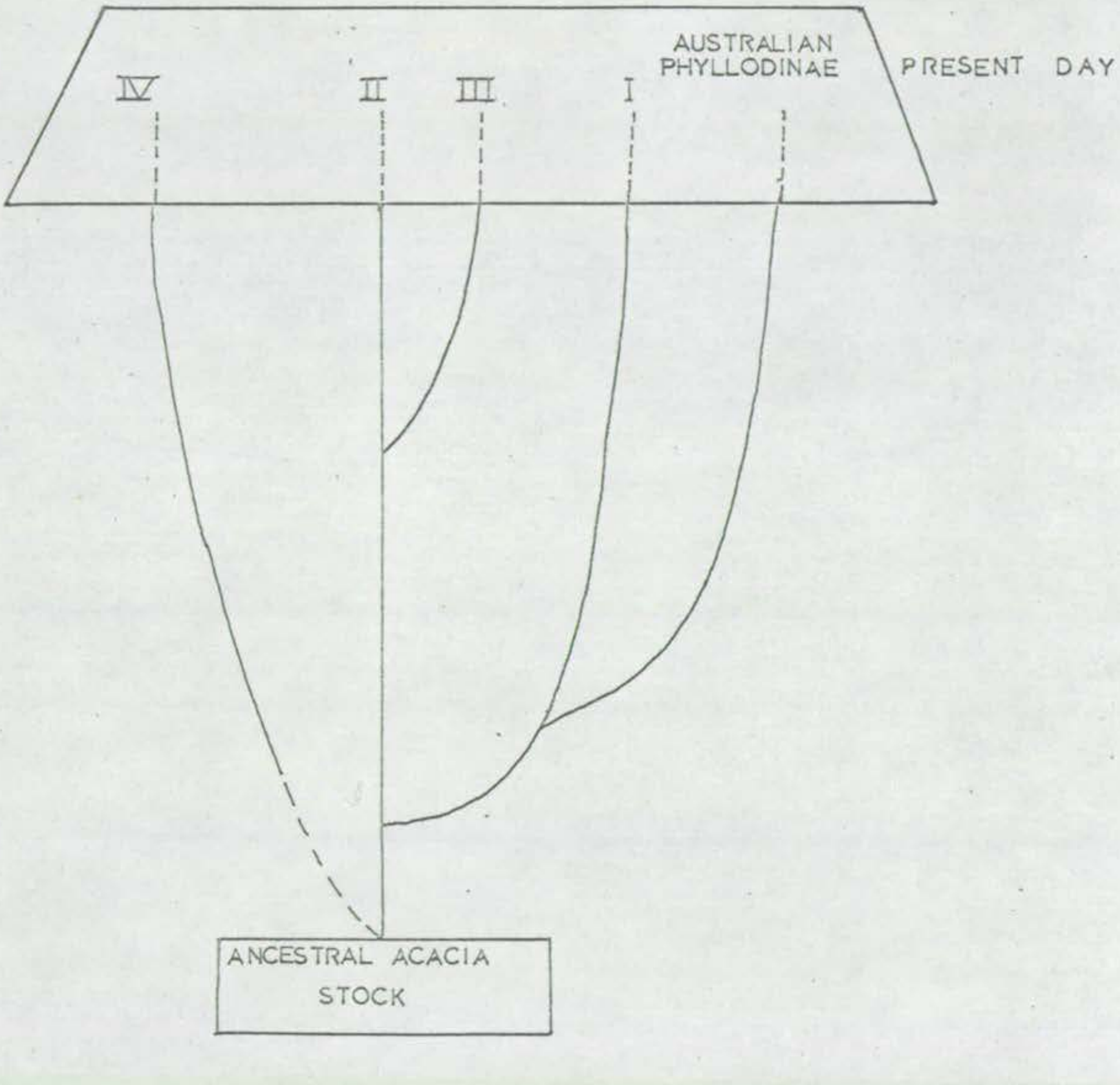


FIG.14 HYPOTHETICAL PHYLOGENETIC TREE OF THE ACACIAS OF THE SUDAN

SUMMARY

This work comprises 31 Sudanese Acacia species and their infraspecific categories. The nomenclature has been brought up to date and the synonyms relating to the Sudan species are cited. A key is provided to separate the species, some of which are further divided into subspecies and varieties. A detailed description is given for the species, giving the full ranges of variation in the country. Two species A. dolichocephala and A. pentagona were added to the Sudan list and the occurrence of A. kirkii is confirmed. There is no existing record of the occurrence of A. venosa mentioned by Andrews (1952).

A detailed study of A. laeta was made to sort out the question of its hybrid origin from A. mellifera and A. senegal, and though its hybrid origin seems probable from the morphologically intermediate position between the two parents, the explanation of its fertile triploidy was left for further cytological investigation.

The anomalous position of A. albida was fully outlined in relation to the other Acacia groups. Though extremely distinct from them, it was retained as a separate monotypic group in Acacia, with no related species.

The geographical distribution of the species in the Sudan was mapped and their occurrence elsewhere in Africa was also mentioned. Morphological correlations were established between the species characters and their distribution in the three main ecological zones: Northern, Central and Southern Sudan.

A subgeneric classification of the Sudan species was produced after an overall consideration of exomorphic and endomorphic characters. The latter

characters were previously neglected in classifying the genus; their correlation with the exomorphic characters in this work produced a better natural classification. The result was the recognition of four major groups and the complete rejection of the traditional classification based on inflorescence types. The highest correlation of attributes was associated with the stipule characters - spinescent or not. The evidence from palynology and anatomy fitted well with the stipule groups. The Acacias with spinescent stipules comprise Group I. The necessity to separate the non-spinescent stipulate Acacias into two groups (II and III) was strengthened by the homogeneity of characters with scale-like and foliate stipules respectively. A. albida, because of its unique features, was put in a separate group (IV).

The proposed classification was found to be workable for the known African species, all of which can be easily accommodated within the four groups. The classification is also applicable to most Asian and American species in addition to the Australian Gummiferae.

This work contains new findings in many fields in the genus, especially in the endomorphic characters: new chromosome counts were made for 16 species, pollen studied for 17 species for the first time, and completely new findings were made in the anatomical field, especially as regards the timber characters. Some of the morphological characters were utilised here for the first time to reinforce group characters, e.g. the pod venation and seed areoles. Studies on seedling development produced much data to strengthen the suggested classification. The difference between stipular spines and exogenous prickles was clearly shown anatomically. The nature of the seed areole was also investigated anatomically: it was shown to mark breaks in the epidermal and pallisade layer of the seed testa associated with water absorption.

The existance of Acacia belts in Central and Northern Sudan was discussed α

and compared with the absence of such belts in Southern Sudan; the centre of diversification of the genus in the country was suggested to be in South-Eastern Sudan.

The relationships of the suggested groups in the studied characters were discussed throughout the thesis and summarised to give an overall correlation of attributes. The effect of habitat was found to be of extreme importance in the evolution of characters; aridity appears to have speeded up evolution of the genus in the Sudan. A cautious attempt was made to discuss certain evolutionary trends, either on the basis of accepted general principles, or on the basis of accepted trends of the genus which were put forward by previous workers.

Due to the limited number of the species studied, a phylogenetic interpretation was difficult. However, a hypothetical tree was put forward based on the relative relationships of the four groups on the basis of what I consider as advanced versus primitive characters found in the present four Acacia groups. This can stand until a more comprehensive work is done in the whole genus on a world wide basis.

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taxon underlined, synonyms not underlined)

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